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The Institute of Marine Science with laboratories at Port Aransas, Texas is a research division of The University of Texas related to the Departments of Bacteriology, Botany, Chemistry, Geology, Physics, and Zoology and the Meteorology Division of the Department of Aeronautical Engineering at the Main University at Austin. An integrated teaching program in graduate marine science is made up of the course offerings from the several departments and from the Institute.

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Effect of the Microbial Production of Hydrogen Sulfide and Carbon Dioxide on the pH of Recent Sediments

CARL H. OPPENHEIMER AND LOUIS S. KORNICKER

Institute of Marine Science
The University of Texas
Port Aransas, Texas

Introduction

Bacteria in recent marine sediments are capable of changing the pH of the environment during their metabolism by the production and decomposition of organic and inorganic acids and bases. The purpose of this paper is to present data which indicate that the pH of recent sediments may be directly related to the presence of bacterially produced hydrogen sulfide and carbon dioxide gases, which dissociate to their respective weak acids. Whereas the acid nature of carbon dioxide and hydrogen sulfide is well known, the behavior of the gases in the complex mixture of natural sediments can not be readily predicted without experimental evidence.

Hydrogen sulfide and carbon dioxide are commonly produced by bacterial activity in recent marine sediments. These two gases dissolve and dissociate in the interstitial water. The production of hydrogen sulfide by the bacterial reduction of sulfates is well known (ZoBell, 1946a; Senez, 1951; and Postgate, 1951). The production of carbon dioxide and carbonates in marine environments has been described by Harvey (1955) and Revelle and Fairbridge (1957).

Laboratory and field experiments were conducted on sediments from the shallow marine bays near the Institute of Marine Science. Experiments are described which show that the saturation of sediments with hydrogen sulfide and carbon dioxide gas results in a lowering of the pH of the sediment. Exposure of the gas saturated sediment to air or inert nitrogen gas is shown to result in an increase in the pH of the sediment. The pH of naturally occurring anaerobic sediments was found to increase after exposure to air, in a manner similar to the results of laboratory experiments. This suggests that low pH values, from 5.4 to 7.6, measured *in situ* in anaerobic sediments can be caused by bacterially produced hydrogen sulfide and carbon dioxide.

Bacterial activity might be a major factor in the early diagenesis of sediment. If bacteria can lower pH and Eh, they can affect both physical and chemical properties of minerals. When bacterial activity ceases, the sediments slowly oxidize. The accompanying increase in pH and Eh will once more affect mineral properties.

The ecological significance of bacterial activity has been pointed out by Mortimer (1941) who has reported changes in the state of certain inorganic compounds during the fluctuation of sediments from the aerobic to the anaerobic state. La Lou (1957) has shown that the precipitation of carbonates may depend on changes in pH caused by microorganisms, where carbonate is precipitated at the anaerobic-aerobic interface or the pH transition area. The changes in pH in sediments may interfere with nutrient

absorption by living organisms by changing the permeability of cellular membranes (Booij and Bungenberg de Jong, 1956, p. 140). Debyser (1952 and 1955) has shown that the *in situ* pH of reduced sediments may be as low as 6.5, and that the decrease in pH is accompanied by an increase in sulfide. Shepard and Moore (1955) have studied the pH, Eh, and organic contents of Texas Coast sediments and show that the increase in organic matter is related to an increase in pH and a decrease in Eh. They also show that the sediments near a river environment have a lower pH than those of bay environments.

Emery and Rittenberg (1952) have related pH to the regeneration of nutrients in sediments of marine basins near the coast of Southern California. They report that many of the cores increased in pH with depth of sediment and that the over-all range in the water and sediments was 7.3 to 8.5. Emery and Rittenberg made pH measurements on sediment samples which were diluted with CO_2 free, distilled water and found that this treatment did not affect the pH. ZoBell (1946b, p. 501) also diluted sediment samples with boiled, distilled water but found that the pH was usually higher for the water plus sediment than for the sediment alone. If hydrogen sulfide or carbon dioxide were diluted or lost during ZoBell's manipulations, one might expect that the pH would rise. It would be interesting to determine the difference between the sediment studied by ZoBell and those by Emery and Rittenberg. Perhaps the difference is due to the differences in hydrogen sulfide and carbon dioxide content.

A recent paper by Carroll (1958) gives data on the changes of pH and Eh which occur in simulated black anaerobic marine mud made with clays. Carroll reports that the pH of the mud rises during incubation, accompanied by a decrease in Eh. The author states that the pH and Eh readings were made each day by removing a small sample. This technique may be reflected by the rather high pH and Eh readings reported, although no mention was made of the method of measuring either Eh or pH. Such an omission of techniques makes it difficult to interpret Carroll's data to compare with the data in our paper.

Methods

All measurements of pH and Eh were made with a Beckman Model G, pH meter fitted with standard heavy duty external electrodes. *In situ* pH measurements in sediments were made by pushing the electrodes directly into the sediment. The electrodes were not pushed beyond eight centimeters because of the possibility of damage. The temperatures of the sediment samples did not vary more than 2° C during the pH measurements. As there is no simple relationship between Eh and pH of sediments the Eh and pH are both specified and no corrections made.

Experiments

Fish Decomposition Experiment

Sediment was obtained from experiments which were being conducted to study the processes occurring during the decomposition of fishes buried in sediments. This sediment, consisting of fine sand with shell fragments, was collected from the Gulf of Mexico beach. The pH of the sediment was 7.6 before the fish were added. The fish were buried approximately 12 cm. below the surface. The sediment surrounding the buried fish gradually turned black probably because of ferrous sulfide. The pH decreased to 6.3 in five

days, from the original value of 7.6. The changes were presumably caused by the activities of the bacteria as they attacked the organic matter of the fish. During this time the Eh of the sediment dropped from the aerobic state, to –300 millivolts (mv.). Hydrogen sulfide gas slowly bubbled up from the area surrounding the fish. A core through the aerobic and anaerobic sediment was collected in a glass tube with an internal diameter of about 4 cm and the sediment was extruded onto a glass plate. The pH of the aerobic and anaerobic part of the core was measured immediately and then at intervals during a three hour period. As shown in Table 1 the pH of the anaerobic section of the

TABLE 1

The Change of pH with Time During Exposure of Sediments to the Air. Aerobic and Anaerobic Sections of a 20 cm. Core Taken from Sediment Adjacent to a Decomposing Fish

Time in min.	pH of Core	
	Aerobic Area from the Surface	Anaerobic Area from 12 cm. Depth
0	7.7	6.7
5	7.7	7.2
15		7.4
45	7.7	8.5
75	7.7	9.2
180	7.7	9.2

core increased from 6.7 to 9.2 during the first 72 minutes. One hundred and five minutes later the pH was still 9.2. The pH of the aerobic sediment remained at 7.7 throughout the three hour period. The pH evidently increased 0.4 units, from 6.3 to 6.7, during the time required for coring, extrusion of the core, and measuring of the initial pH of the core.

SATURATION OF SEDIMENT WITH HYDROGEN SULFIDE AND CARBON DIOXIDE

The anaerobic section of the core was dried at room temperature for 48 hours. Distilled water was added to the dry sediment to provide the approximate original water content. The pH of the rehydrated sediment was 8.5. The sediment was separated into two aliquots. Hydrogen sulfide was bubbled through one aliquot and carbon dioxide was bubbled through the other. The gas saturation was carried out in a stoppered bottle with two glass tubes inserted into the stopper. The tube through which the gas was introduced penetrated the sediment in the bottom of the bottle. The other tube did not come into contact with the sediment and served as an outlet for excess gas. The stopper was then removed, a jet of nitrogen gas was blown into the bottle, and pH electrodes were inserted into the sediment. The nitrogen gas flushed air, which could oxidize the reduced sediment, from the sediment and also helped flush hydrogen sulfide and carbon dioxide out of the sediment. The sediment was stirred every 5 minutes and the pH measured at short intervals over a three hour period. The data are presented in Figure 1.

The pH of the rehydrated sediment decreased from 8.5 to 6.8 when saturated with H_2S, and from 8.5 to 6.1 when saturated with CO_2. The pH values then increased at a constant rate during nitrogen flushing. A straight line was obtained when the pH values were plotted against the square root of time (Fig. 1).

FIELD EXPERIMENTS

During laboratory experiments described above, the pH of anaerobic sediment rapidly increased when the sediments were exposed to air. The next step was to determine if an

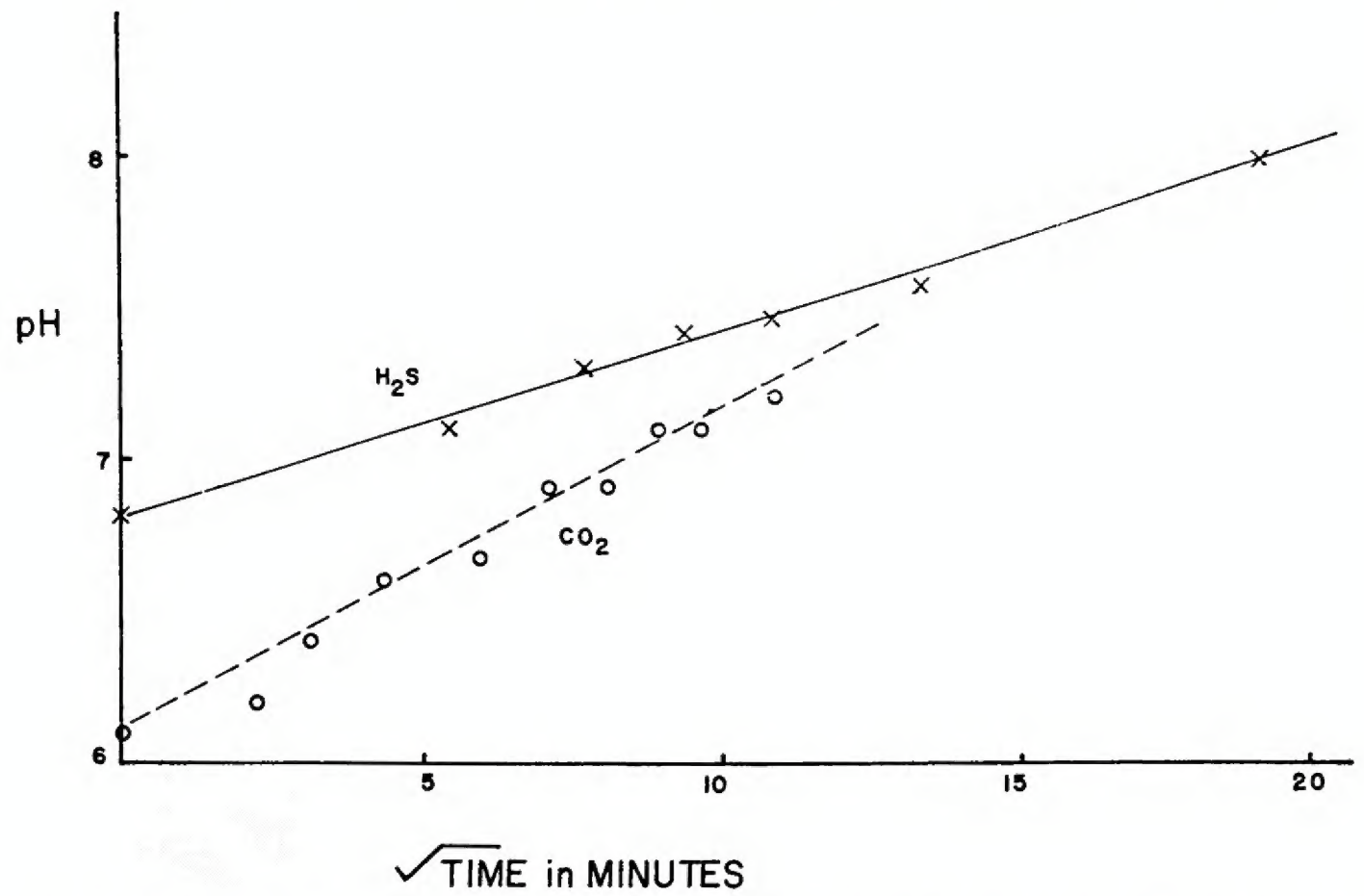

FIG. 1. Change of pH with square root of time for hydrogen sulfide and carbon dioxide gas saturated sediment after exposure to an atmosphere of nitrogen.

TABLE 2

In situ Values of pH and Eh in Millivolts (mv.) in Marine Sediments near Corpus Christi, Texas and Sapelo Island, Georgia

Station		Depth of Measurements in cm.					
		Surface	1	2	4	6	8
Aransas Bay near Corpus Christi	pH	9.0	7.9	6.6	6.6	6.6	6.6
	Eh	....	+144	+44	+44	....	—276
Aransas Bay near Corpus Christi	pH	9.2	8.6	7.6	6.8	6.7	6.7
	Eh	....	+4	—156	....	....	—300
Aransas Bay near Corpus Christi	pH	8.6	....	....	6.6	....	6.5
	Eh	....	....	....	—136	....	—256
Aransas Bay near Corpus Christi	pH	8.4	....	8.0	6.9	6.5	6.5
	Eh	....	+74	—36	—36	—146	—236
Corpus Christi Bay	pH	8.0	7.1	....	6.8	6.7	6.7
	Eh	....	—186	—286	....	....	—306
Mustang Island	pH	8.4	7.1	7.0	6.7	6.8	6.7
	Eh	....	—226	—256	—156	—56	—91
Sapelo Island							
Station 1	pH*	8.2	6.9	....	6.3	....	5.9
Station 2	pH*	8.4	....	6.8	5.4	....	5.4

* (Eh was not measured in Sapelo Island sediments. Abundant H_2S was present and it is assumed that the core below the surface was anaerobic.)

increase in pH occurred when samples of anaerobic sediment collected in natural environments are exposed to air. Several locations containing anaerobic sediments were selected from the shallow marine bays near the Institute of Marine Science. Measurements of pH and Eh were made directly in the sediment in order to obtain *in situ* pH and Eh measurements. A core was collected in a 5 cm plastic tube in the area adjacent to where the electrodes were inserted. Changes in pH were measured when the core was exposed to the air.

Sediments from Corpus Christi Bay, Laguna Madre, Aransas Bay, Mustang Island, Texas and Sapelo Island, Georgia, were examined. The *in situ* pH and Eh of the sediments are given in Table 2. The pH values appear to vary directly with the Eh values. Whereas the Eh might be expected to decrease with rise in pH (ZoBell, 1946b), a reverse relationship was found. In all anaerobic sediment tested the pH increased when the sediments were exposed to the air. A typical series of measurements made in the field are presented in Figure 2 and Table 3 which show the change in pH with time. The data in

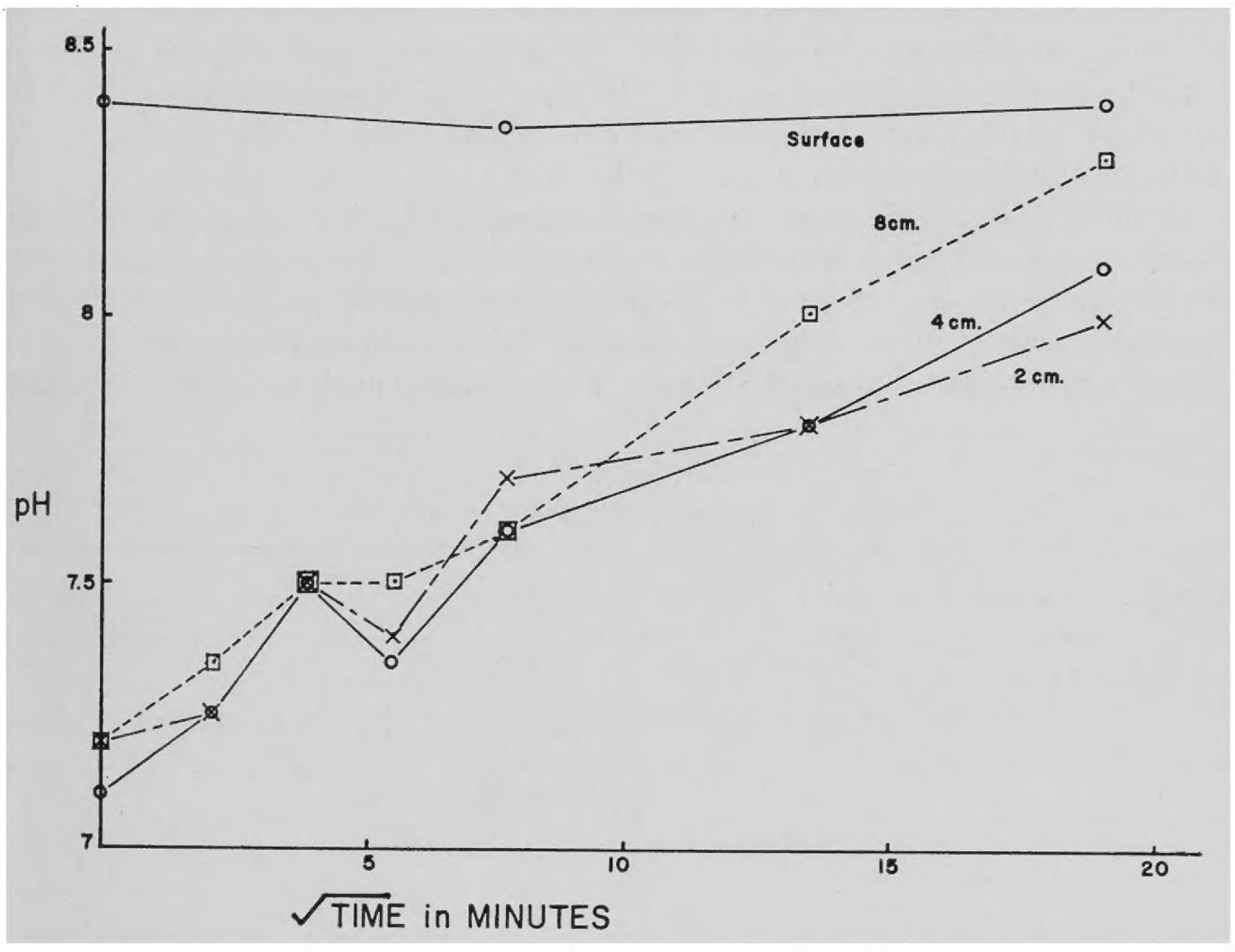

FIG. 2. Change of pH with the square root of time for a core removed from anaerobic sediment on Mustang Island. Measurements were made at the indicated depth measured from the top of the core.

Figure 2 are plotted against the square root of time. The amount of pH increase varied from sediment to sediment and suggests that the net increase might be proportional to the amount of hydrogen sulfide and carbon dioxide present in the sediment at the time of collection. Anaerobic marsh sediments from Sapelo Island, Georgia, with more acid pH, showed a similar increase in pH when sections of the sediment were exposed to air.

It was immediately apparent that the rate at which the pH increased was influenced by the manner in which the core was treated. If the core was broken open and disrupted during the pH measurements, the pH changed more rapidly. If the holes in the

TABLE 3

The Changes in pH Which Occurred in Disturbed and Undisturbed Cores of Sediments from Laguna Madre After Exposure to the Air

Core Depth cm.	Measurements *in situ* Eh (millivolts)	pH	pH in a Disturbed Core — Minutes after collection: 5	15	25	35	60	pH in an Undisturbed Core — Minutes after collection: 20	40	Description of Sediments
Surface	+244	8.2	8.2	....	....	....	8.2	....	....	Coarse sand
0.5	+ 84	7.2	7.2	....	....	....	7.2	....	....	Sandy shell
2	—264	7.0	7.8	8.0	....	8.5	8.2	7.6	8.1	Sandy shell
6	—246	7.0	7.7	7.5	7.9	8.1	7.9	7.2	7.3	Clay silt with decaying algae
8	—266	7.2	7.8	8.1	8.7	8.7	8.4	7.1	7.5	Fine sand

sediment where the electrodes were inserted were covered up after the electrodes were removed, the rate of change of pH was reduced. This is illustrated in Table 3 which gives field data on the pH of cores which were disturbed by the intermittent insertion of the electrodes and adjacent cores which were extruded but not otherwise disturbed before the pH was measured. The pH in the undisturbed cores changed more slowly than the pH of the disturbed core. This is considered to be the result of a more rapid release of gases from the disturbed core.

During the *in situ* field experiments, there was some indication that a small but rapid change in pH took place immediately when cores were removed from the sediment. Measurements of pH were made *in situ* and on cores approximately one minute after they were removed from the adjacent sediment. The pH increased from 0.1 to 0.4 units above the *in situ* values (Table 4). Measurements were also made on sealed stored cores

TABLE 4

Changes in pH in Sediments during Collection

Sample	Depth	pH Measurement: *in situ*	One Minute after Collection	2–4 hrs. after Collection
Unstoppered Samples:				
1	3	6.6	6.8	....
	7	6.6	6.8	....
2	6	6.5	6.6	....
	8	6.5	6.5	....
3	6	6.3	6.7	....
Cores Collected in Plastic Tubes, Stoppered, Extruded in Laboratory:				
1	6	6.7	....	7.3
	8	6.7	....	7.1
2	4	6.7	....	7.1
	8	6.7	....	7.2

which were collected in plastic tubes, tightly stoppered, stored for from 2 to 4 hours and then extruded. The pH measured one minute after the cores were extruded was 0.4 to 0.6 units above the original *in situ* values (Table 4b).

Discussion

The data contained in this paper illustrate ways that pH can be increased or decreased by the addition or removal of hydrogen sulfide and carbon dioxide from sediments. The increase in pH shown in Figure 2, which occurred after natural anaerobic sedi-

ments were removed from their environment, was similar to the increase shown in Figure 1 which took place when hydrogen sulfide and carbon dioxide in artificially gas saturated sediments escaped from the sediment samples in the laboratory.

Data from experiments with decomposing fish indicate that the area adjacent to the fish where hydrogen sulfide was observed became more acid. When the sediment was removed from near the fish, the pH rapidly increased (Table 1) to a level higher than the original pH of the sediment before the decomposition started.

Diffusion Processes

The increase in pH for both laboratory and field experiments was linear with the square root of time. As shown by Höber *et al.* (1945, p. 10) gas diffusion processes have a linear function with the square root of time. This indicates a similarity between the gas diffusion process and the experimental increase in pH described in this paper. However, since pH is a logarithmic function, the linear change in pH may actually be the result of dissociation of the gases, or an equilibrium between the dissolved and ionic state of the gases.

Diffusion rate of gases through sediment is governed by Fick's Law and thus is dependent on the amount of interstitial water, density of the gas, temperature, agitation of the sediment, salt content, amount of colloidal and dissolved organic matter and the abundance, size, and arrangement of interstitial spaces of the sediment. These factors probably account for variations in the amount of pH increase found in various places and depths of sediment when the sediments are exposed to air. The data from Table 3 show how the pH change is more rapid for disturbed cores as compared to undisturbed cores. The permeability and amount of water present may influence the rate of diffusion. Sediments composed of small particles normally have a larger water content than sediments composed of large particles (Pettijohn, 1949: 67), and one might expect more gas to diffuse from finer sediments, such as clays, at a faster rate. However, small particles of one micron and smaller will have a greater proportion of, or perhaps all, the water in the bound state, and thus the diffusion rate may be lower (See Szent-Györgyi, 1957: 35).

The diffusion coefficient of a gas affects the slope of a curve of pH plotted against the square root of time but does not change the linearity. The variation in slope in Figure 1 suggests that the effects of the diffusion of hydrogen sulfide and carbon dioxide from sediment are different.

The CO_2 saturated sediment has a pH of approximately 6.1 whereas the H_2S saturated sediment has a pH of 6.8 as shown in Figure 1.

Dissociation Constant for Hydrogen Sulfide and Carbon Dioxide

The dissociation constant for CO_2 (as H_2CO_3) in sea water, $K_1 = 0.26$ to 1.12×10^{-6}, varies with the chlorinity and temperature as summarized by Harvey (1955, p. 166). The pH of CO_2 saturated sea water may be calculated by equation 2 of Harvey (p. 172). With 1 atmosphere partial pressure of CO_2, at 30° C and chlorinity of 19 parts per thousand the calculated pH is 5. This figure is somewhat lower than the experimental value given in Figure 1. In sediments the partial pressure of the gas may be lower than 1 atmosphere and a relatively higher pH should result.

The K_1 dissociation constant of H_2S in fresh water at 25° C is 5.7×10^{8}. According to Hutchinson (1957, p. 759, water, subjected to a pressure of 1 atm of H_2S, will have a

pH of approximately 4. The addition of base substances will cause a rise in the pH. Thus the pH will be a function of the continued supply of the weak acid of H_2S to the buffering capacity of the system.

Changes in pH Observed in Sediments

The pH increase observed after anaerobic sediments are exposed to atmospheric condition is quite rapid. The data in Table 4 show that a small change in pH takes place within the time required to measure the pH (e.g. 1 min.) and that a small change in pH also takes place in sediments stored in plastic tubes which are sealed with rubber stoppers at end. This change probably occurs as the sediments immediately react to agitation and exposure to air. Therefore one can assume that the low pH is not principally caused by non-gaseous inorganic or organic acids which would diffuse very slowly. However the over-all pH of any sediment will depend not only on the presence of carbon dioxide and hydrogen sulfide but on the balance of all the acid or basic constituents of the sediments, for many of the by-products of bacterial activity may be organic acids.

The data in Table 2 representing measurements from several locations in the bays show that a low Eh is accompanied by a relatively low pH, as compared with the surface pH. Sediments used in this study were selected from field areas which were rich in sulfides in order to get large variations in Eh within a short core. The senior author has made several hundred *in situ* measurements of Eh and pH (unpublished) in various sedimentary environments and has found no general trend in Eh as plotted with depth. Some reduced sediments without H_2S do not have a low pH and some cores with reduced areas near the surface became more oxidized with depth. Debyser (1952, 1955) and Wheatland (1954) have reported that whereas the pH of some anaerobic sediments which contained hydrogen sulfide decreased with depth, others increased. Debyser did not state how his samples were handled during the pH measurements.

The data in Table 2 also show that the pH of the surface of the sediments varied from 8 to 9.2. This relatively high pH on the surface of those moist marine sediments may have been caused by photosynthetic activities of the mat of unicellular flagellates, diatoms and other algae which were present. Carbon dioxide, which is used as a carbon source by the plants, is removed from dissolved bicarbonate ions leaving an excess of hydroxyl ions (Rabinowitch, 1951, p. 899).

Some investigators (Rittenberg, Emery, and Orr, 1955, p. 33; Revelle and Fairbridge, 1957, p. 282) have published information which indicates that pH values up to 8.5 are found in anaerobic sediments.

The anaerobic sediments studied increased in pH when they were removed from their natural environment. The change was usually quite rapid. It is very possible that pH values of 7 and above reported in the literature for anaerobic sediments may be the result of the pH having increased because of the manner in which the cores were handled before the pH was measured.

The microbiologist has been able to determine the number and types of bacteria in sediment but has not been able to relate the population to activity. The amount of pH increase when anaerobic sediments are exposed to the air may be an index of the amount of activity of microorganisms in the undisturbed sediment, a large increase in pH representing a large microbial activity.

Bacterial Activity and pH

The data from our experiments indicate that the pH of natural sediments may be lower than that anticipated according to reactions obtained from pure culture work on sulfate reducing bacteria such as described by Senez (1951 and 1953). According to Senez, the hydrogen for the reduction of sulfate to sulfide by sulfate reducing bacteria may be provided from organic matter or hydrogen gas according to the following reactions:

$$2CH_3CHOHCOOH + 2H_2O + 2H^+ + SO_4^{--} = 2CH_3COOH + 2CO_2 + H_2S + 4H_2O \quad (1)$$

$$2H^+ + SO_4^{--} + 4H_2 = H_2S + 4H_2O \quad (2)$$

Both reactions from controlled experiments should result in a loss of hydrogen ions and a production of weak acids with a resulting net increase in pH. Revelle and Fairbridge (1957, p. 282) also state that the removal of the strong acid sulfate ion and the replacement with sulfide, a weak acid, should result in a rise in pH. However, it must be emphasized that changes in sulfate content alone will produce only small changes in pH as compared to changes in hydrogen ion concentration. The results in this paper of a lowering of pH during fish decomposition and hydrogen sulfide and carbon dioxide production show that sulfate reduction apparently is not accompanied by a decrease in hydrogen ion concentration. Perhaps the bacterial reduction of sulfate to sulfide may take place in nature as shown by the following reaction:

$$2CH_3CHOHCOOH + 2H_2O + Ca^{++} + SO_4^{--} = 2CH_3COOH + CaCO_3 + H_2S + CO_2 + 3H_2O \quad (3)$$

The pH according to equation 3 would be lowered by bacterial sulfate reduction, providing the hydrogen sulfide and carbon dioxide remain dissociated in the sediment. In order for this reaction to take place, calcium carbonate would have to precipitate. Shepard and Moore (1955) and Ginsburg (1957) state that carbonates are often found in acid sediments so this limitation may not be serious in nature.

Emery and Rittenberg (1952) state that pH may be dependent on the bacterial conversion of organic matter and the nature of organic by-products illustrated by H_2A and A in the equations:

$$4H_2A + SO_4^{--} = S^{--} + 4A + 4H_2O \quad (4)$$

where A represents some oxidizable organic compound. For example, if H_2A is an alcohol the resulting production of 2 moles of acetic acid for each mole of sulfate reduced should produce a decrease in pH. However, our results indicate that dissolved gases (H_2S and CO_2) are the major factors affecting pH rather than organic acids.

The senior author has made pH measurements on an enriched culture containing sulfate reducing bacteria in sediments with lactate as an energy source. The pH decreased from 8.3 to 6.5 in three days and then started to rise reaching a pH of 7.5 in three days. This might be explained by metabolic by-products being accumulated during growth and the initial pH regulation by H_2S or CO_2 overshadowed by alkaline metabolic products.

Summary

1. The pH of sediments decreases when hydrogen sulfide and carbon dioxide are bubbled through the sediment or when the gases are produced in the sediment during the bacterial decomposition of fishes.

2. The sediments saturated with hydrogen sulfide or carbon dioxide increased in pH linearly as a function of the square root of time when the sediments were exposed to an atmosphere of nitrogen gas. The increase in pH is considered to be caused by the escape of the gases from the sediment. The diffusion rate increased when the sediments were disturbed.

3. The similarity in the manner and rate at which pH increased in sediments impregnated with the gases and anaerobic sediments obtained in natural and simulated natural environments, suggests that the change in pH values in the latter is caused by a loss of hydrogen sulfide and carbon dioxide. Low pH values obtained in anaerobic sediments in nature are due at least in part to the presence of hydrogen sulfide and carbon dioxide. Both gases are produced during microbial decomposition of organic matter.

4. The fact that samples of anaerobic sediment seem to increase in pH immediately after removal from the ground casts doubt upon the reliability of numerous pH values reported in the literature from determinations of pH made on sediments carried from the sampling area to the laboratory. *In situ* determination of pH seems to be the only reliable way of obtaining accurate pH values of anaerobic sediments.

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Comparative Studies on the Metabolism of Marine Waters[1]

HOWARD T. ODUM AND CHARLES M. HOSKIN

Institute of Marine Science
The University of Texas
Port Aransas, Texas

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Introduction

Each day as the sun rises and retires the beautiful green bays like great creatures breathe in and out. By day photosynthetic production of food and oxygen by plants is plentiful, but day and night there is also a furious feasting. The animals, the consumer parts of plants, and the bacteria remove the food and oxygen previously created from the sunlight. On some days the production exceeds the respiratory consumption, and organic food matter accumulates, but at other times respiration dominates so that the

[1] These studies were aided by the Rockefeller Foundation.

waters and their bottom oozes lose their store of energy. Just as the life in single organisms is driven by the metabolism of the body cells, so many marine phenomena of theoretical or practical interest to man can be related to the composite metabolism of the environment. All through the year photosynthetic metabolism provides necessary chemical fuels for food chains, fisheries, sport of man, oyster reefs, plant beds, duck foods, dissolved oxygen for counteracting pollution, and biological activity that consumes and binds radioactive fallout to organic matter. Even the geochemical cycles are driven by the community metabolism which alternately binds and releases carbon-dioxide, nitrogen, phosphorus, and many trace elements. The organic matter and oil left in past ages in the marine sediments may be understood only by interpreting the metabolism of past seas.

It is thus a first step in logical conservation as well as for scientific understanding to know the nature of the community metabolism. From metabolic rates may be estimated the magnitudes of dependent processes. Sensible management based on maintenance of fertility is a principal by-product of community studies in marine ecology.

In this paper, metabolic methods are used for rapid study of whole water areas. Measurements of metabolic rates in contrasting waters indicate qualitative contrasts and a wide range of values in quantitative data. Such data can provide understanding of shallow marine bay systems anywhere and a basis for resolving conflicts for conservation leadership.

Diurnal curves of oxygen and carbon-dioxide (or pH) are numerous in the literature. Many recent efforts are being made to convert these data into metabolism figures. In addition to the papers cited in previous reviews (Odum, 1956, 1957a), there are the following: in lakes: Jackson and McFadden (1954), Talling (1957), and Vinberg whose work in 1940 is quoted by Talling (1957); in marine waters: Sugiura (1953, 1956), Kohn and Helfrich (1955), and Ryther (1958); and in streams: McConnell (1958), Hoskin (1957), and Hornuff (1957). In this paper the diurnal curve method for measuring metabolism is widely applied in coastal waters with a number of tests of the methods.

Acknowledgement

We are grateful to the many persons who have helped with the laborious day-night sampling including Dr. W. McConnell, University of Arizona; Dr. Louis Kornicker, Institute of Marine Science; and Mr. William Guest and Mr. Richard Hoese, Texas Game and Fish Commission. Mr. Kilho Park and Mr. Herbert Bruce of A & M College of Texas cooperated in the diurnal curve work concurrently with the pH studies reported elsewhere (Park, Hood, and Odum, 1958) and Mr. Thomas Hellier, Jr. aided with the Laguna Madre series. We are grateful for further testing of methods by the oceanography class, Duke Marine Laboratory, 1956 and the biological oceanography class at the Institute in 1957. Bell jar and tank experiments were supported by the National Science Foundation grant on Ecological Microcosms. We are grateful to Mr. M. Lerner for courtesy at Bimini. The Gulf Oil Company helped us in the oil tower work. Tanks were made available by Dr. A. Chestnut, Institute of Fisheries, University of North Carolina, Morehead City. These studies were begun at the Duke Marine Laboratory, Beaufort, North Carolina.

Methods

For measurement of the overall metabolism, dissolved oxygen values representative of the free water were measured by means of the Winkler method by an observer in a small boat through a 24 hour period. Then as previously described (Odum, 1956) rates of diffusion, respiration, and gross photosynthesis were computed graphically. The light and dark oxygen bottle methods for measurement of plankton metabolism were also used at each station. In the Texas bays so far tested, the gentle drift of the water over flat bottoms tends to provide ideal conditions for adequate mixing for the diurnal curve method for measuring community metabolism.

Since the marine estuaries and ponds are not entirely homogeneous, the reproducibility and variation of the measurements had to be determined. Replication of all the diurnal curves was not possible because of the labor, but duplicate curves from contrasting stations were obtained for Mesquite Bay (Table 2) July 22, 1957, and 3 separate stations in the upper Laguna Madre were run by W. McConnell on Jan. 22, 1958. The metabolic values in gm. Oxygen/M^2/day for the three stations ½ M deep in the Laguna Madre are given below. Diffusion constant is given in gm./M^2/hr. at 0 per cent saturation (K).

	P	R	K
Reds Camp, 5th post	2.1	2.7	0.3
Reds Camp, K. Park's station	2.5	2.6	0.3
Reds Camp, 1957 station	1.9	1.9	0.5

For the convenience of others planning to use the diurnal curve methods and in response to requests, instructions are given below with a sample calculation (Fig. 1).

Instructions for Measurement of Community Metabolism with the Diurnal Curve Method

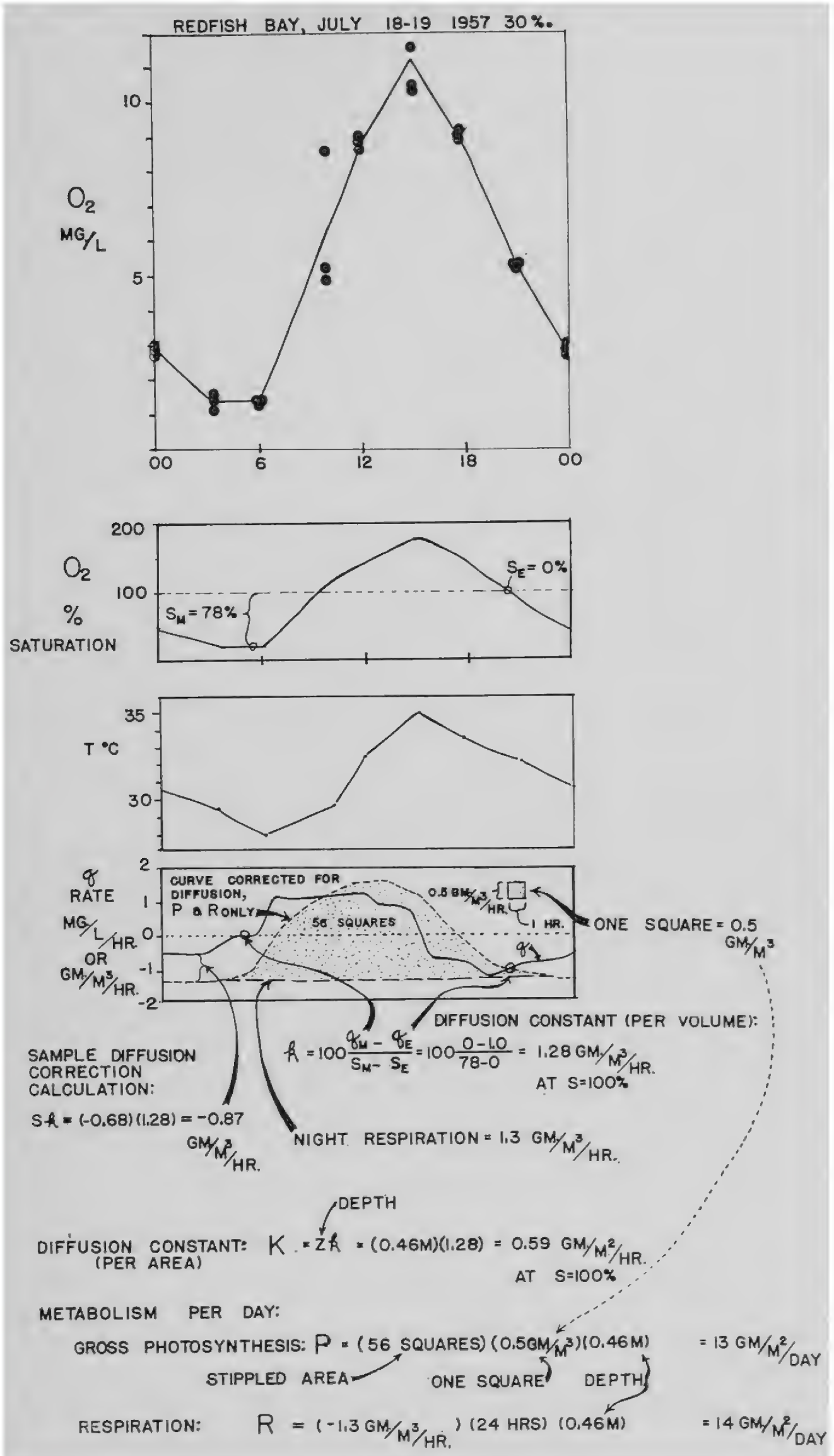
1. Locate an area of representative depth in which the history of the water moving into the area will be similar to the history of the water moving away. Circulation should be gentle as created with slowly drifting current and gentle wave action. Use fluorescein dye spread on the surface to determine the degree of vertical circulation. The dye will become vertically dispersed throughout the layer in 1–5 minutes in a suitable area. If the water is vertically stratified as indicated by temperature stratification, samples must be taken at several levels (Fig. 2). If it is a new area not previously tested, run several stations to determine if a single station is representative of the water mass (Fig. 3).

2. Sample and analyze with the Winkler method for dissolved oxygen every three hours for a duration of 24 hours. At each time of sampling, collect duplicates or triplicates, preferably separated by a minute of time. Express data as mg./liter so that ready conversion to gm./M^2 can be made simply by multiplying by depth. At each sampling also obtain temperature, depth, and some estimate of current; collect two salinity samples during the period. Determine the average depth in the trajectory and during the period.

3. Plot oxygen and temperature curves as shown in Figure 1. From tables of oxygen saturation for given temperature and salinity determine the percent saturation and plot

---

Fig. 1. A typical diurnal curve and sample calculation for determination of gross photosynthesis (P), community respiration (R), and diffusion constant (K). Redfish Bay, Port Aransas, Texas, July 18–19, 1957. Calculations are included on the face of the graph. See text for explanations.


REDFISH BAY, JULY 18-19 1957 30‰
10
5
O2
MG/L
00
6
12
18
00
200
100
O2
%
SATURATION
SM = 78%
SE = 0%
35
30
T °C
2
1
0
-1
-2
q
RATE
MG/L/HR.
OR
GM/M3/HR.
CURVE CORRECTED FOR DIFFUSION, P & R ONLY
56 SQUARES
0.5 GM/M3/HR.
1 HR.
ONE SQUARE = 0.5 GM/M3
DIFFUSION CONSTANT (PER VOLUME):
k = 100 (qM − qE)/(SM − SE) = 100 (0 − 1.0)/(78 − 0) = 1.28 GM/M3/HR. AT S=100%
SAMPLE DIFFUSION CORRECTION CALCULATION:
Sk = (-0.68)(1.28) = −0.87 GM/M3/HR.
NIGHT RESPIRATION = 1.3 GM/M3/HR.
DEPTH
DIFFUSION CONSTANT: (PER AREA) K = Zk = (0.46M)(1.28) = 0.59 GM/M2/HR. AT S=100%
METABOLISM PER DAY:
GROSS PHOTOSYNTHESIS: P = (56 SQUARES) (0.5 GM/M3) (0.46M) = 13 GM/M2/DAY
STIPPLED AREA
ONE SQUARE
DEPTH
RESPIRATION: R = (-1.3 GM/M3/HR.) (24 HRS) (0.46M) = 14 GM/M2/DAY

a saturation curve (Fig. 1). See Steen (1958) for discussion of various tables available. Use millimeter graph paper for these graphs, since many subdivisions are necessary for counting squares.

4. From the oxygen graph, using a running two hour interval, determine the rate of oxygen change in mg./liter/hr.; plot the rate values just below the other graphs on the same horizontal time scale. A two hour computation interval provides some smoothing of the sharp corners of the oxygen curve eliminating artifacts that come from infrequent sampling.

5. Determine the diffusion constant from the rate of change graph (lower graph in Figure 1) with the use of two points, one in the predawn period (q_m) and one in post sunset period (q_e). Use care in choosing the points; do not take an irregularity or point known to be atypical due to sudden change of wind or other variable. The diffusion constant per volume is k. Little letters are used for volume; capital letters for measurements per area. In mg./1/hr. at 0 per cent saturation k may be computed as follows:

$$k = 100\frac{q_m - q_e}{S_m - S_e}$$

where q_m is rate of change at a time before dawn in mg./l/hr.

q_e is rate of change at a time after sunset in mg./l/hr.

S_m is the percent saturation deficit before dawn at the time chosen for calculating q_m. (78 percent in example in Fig. 1).

S_e is the percent saturation deficit after sunset at the time chosen for calculating q_e. (0 percent in example in Fig. 1).

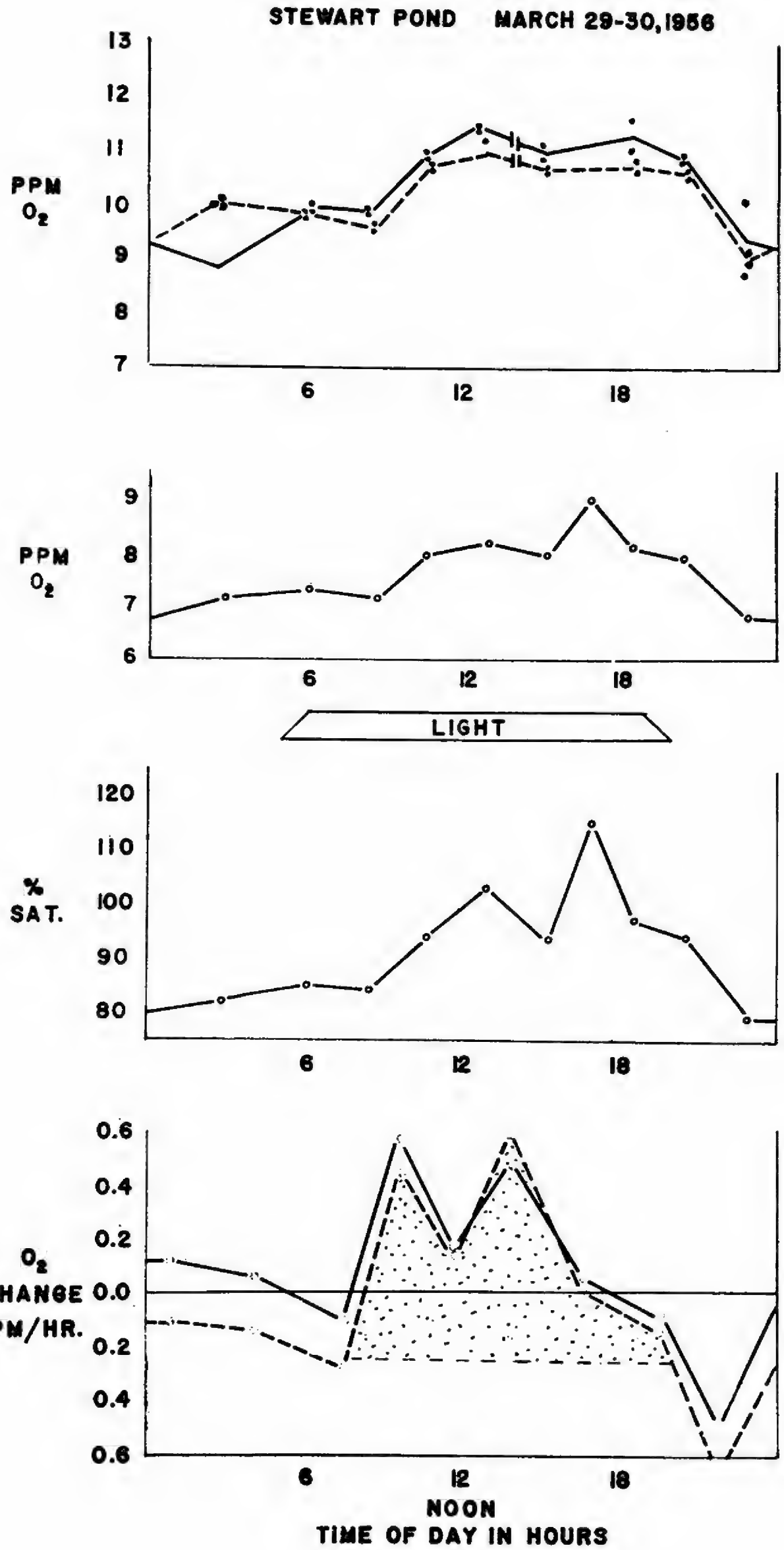
K, the area based diffusion constant, may be obtained by multiplying by the depth (Z) in meters. K in gm./M^2/hr. at 0 percent saturation has been found to be: 0.1 to 1 in quiet waters, waters less than ½ M. deep, or stratified waters; 1 to 3 in bays with gentle circulation and wave action; and 3 or more in strong currents and large waves. In the example in Figure 1 sample calculations are given with result that k is 1.28 gm./M^3/hr. at 0 percent saturation (100 percent saturation deficit). At 0.46 meters depth K is 0.59 gm./M^2/hr. at 100 percent saturation deficit.

6. On the rate of change curve multiply the saturation deficit by k (volume diffusion constant) and add or subtract from the rate of change curve graphically so as to replace oxygen which diffused out or to retract the oxygen which diffused in. This is done in the example in Figure 1. One multiplication is given for a predawn point in Figure 1. The new curve includes community metabolism corrected for diffusion (dashed line in Fig. 1); it is the curve which might have resulted had there been no diffusion.

7. On the corrected curve determine the community respiration line by drawing a smoothed line through the average of the nighttime rate of change points. See example marked in Figure 1. Extrapolate this across the daytime period. In so doing one assumes nighttime respiration similar to daytime respiration which is probably not correct. It is possible to make this line in some different shape as soon as it is determined what the

---

FIG. 2. Diurnal curve of oxygen for Stewart Farm Pond, Durham Co., North Carolina, March 29–30, 1956. Curves for two depths are drawn in the upper graph, but computations are based on an average of all depths in the second graph. In the lower graph the dashed line has been corrected for oxygen diffusion.

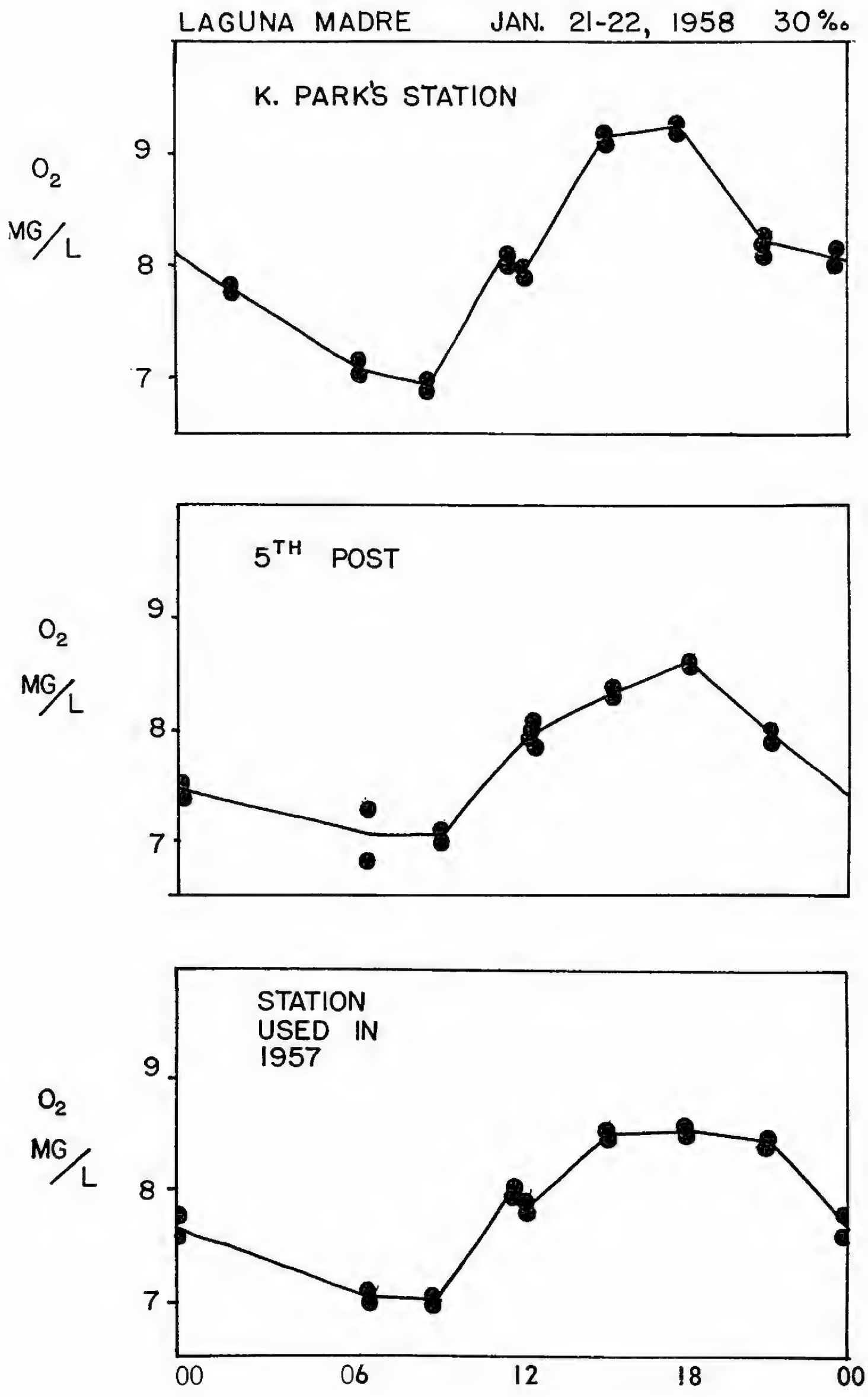

STEWART POND MARCH 29-30, 1956
PPM O_2
13
12
11
10
9
8
7
6
12
18
PPM O_2
9
8
7
6
6
12
18
LIGHT
%
SAT.
120
110
100
90
80
6
12
18
O_2
CHANGE
PPM/HR.
0.6
0.4
0.2
0.0
0.2
0.4
0.6
6
12
18
NOON
TIME OF DAY IN HOURS

usual shape of daytime community respiration is. The average rate of respiration multiplied by the depth and the number of hours (24) yields community respiration rate (R) in gm. oxygen/M^2/day. See example of calculation in Figure 1. Values are best left in oxygen rather than converted fictitiously to carbon or glucose. For rough purposes grams of oxygen are almost the same as grams organic matter; further conversion is unrealistic unless the respiratory quotients and chemical nature of the community organic matter are known in some detail.

8. The area between the respiration line and the daytime hump of the corrected rate of change curve is the gross community photosynthesis including simultaneous respiration of the community. This area is stippled in Figure 1. Determine the gm./m^3 value of one square on the graph paper by multiplying the dimensions of the square. For example, in Figure 1 the square has dimensions 0.5 mg./l/hr. in the vertical and 1 hr. on the horizontal time axis. The product, 0.5 mg./l, is the metabolic value of one square on the graph paper. The stippled area contains 56 such squares. Count the squares and multiply by the gm./M^3 per square and depth in meters to obtain the gross production (P) in gm./M^2/day oxygen. In the example in Figure 1 P is 13 gm./M^2/hr. Both the respiration and the photosynthesis are much affected by the choice of the respiration line. The accuracy of the method is probably limited by this step. In some smooth curves (Fig. 1), there is little doubt and one has no choice in drawing the respiration line. In some graphs in which points are very irregular, some subjectivity is introduced (example, Fig. 4), and results are held with less confidence, although the confidence interval can be estimated visually. It is probable that community respiration is actually varying as suggested by CO_2 curves (Park, Hood, and Odum, 1958).

9. If several different stations have been run, the oxygen curves should be superimposed. If the differences are small, the data should be lumped and the combined curve used as the general curve for the water mass. If large differences are found, indicating heterogeneity in the communities, the results cannot be considered as accurate. In such cases the curve for one station does not represent metabolism at that station unless the water was stationary. The basic assumption in diurnal curve analysis (not considering the entirely different conceptual approach used for springs; Odum, 1956, 1957a) is that the water measured at a station has had a recent metabolic history characteristic of the water measured at the station during the previous sampling. If the water moving in has a different content of oxygen from the water which simultaneously leaves the station, results will be in great error. The underestimation of trajectory effect is the principal danger in the uncritical use of the diurnal curve method. For detailed work in a new area, the worker is obligated to present duplicate station results in order to establish the degree of uniformity of the body of water. In the diurnal curve method metabolic rates are computed on a volume of water basis and converted to an area basis by multiplying by the average depth. Where possible an average depth should be determined with careful morphometric measurements. Such measurements for example were made in Prytherch's lagoon (Fig. 5) and Stewart Farm Pond (Fig. 2). In most of the data on Texas bays, however, the depth of the station has been used as a first approximation of the depth of the water mass measured. Even though Texas bays are remarkably flat

FIG. 3. Simultaneous diurnal curves at three different stations in the upper Laguna Madre near Reds Fish Camp as obtained by William McConnell, January 21–22, 1958. See text for values of metabolic rate and diffusion constant.


LAGUNA MADRE JAN. 21-22, 1958 30 ‰
K. PARK'S STATION
O_2 MG/L
9
8
7
5TH POST
STATION USED IN 1957
00
06
12
18
00

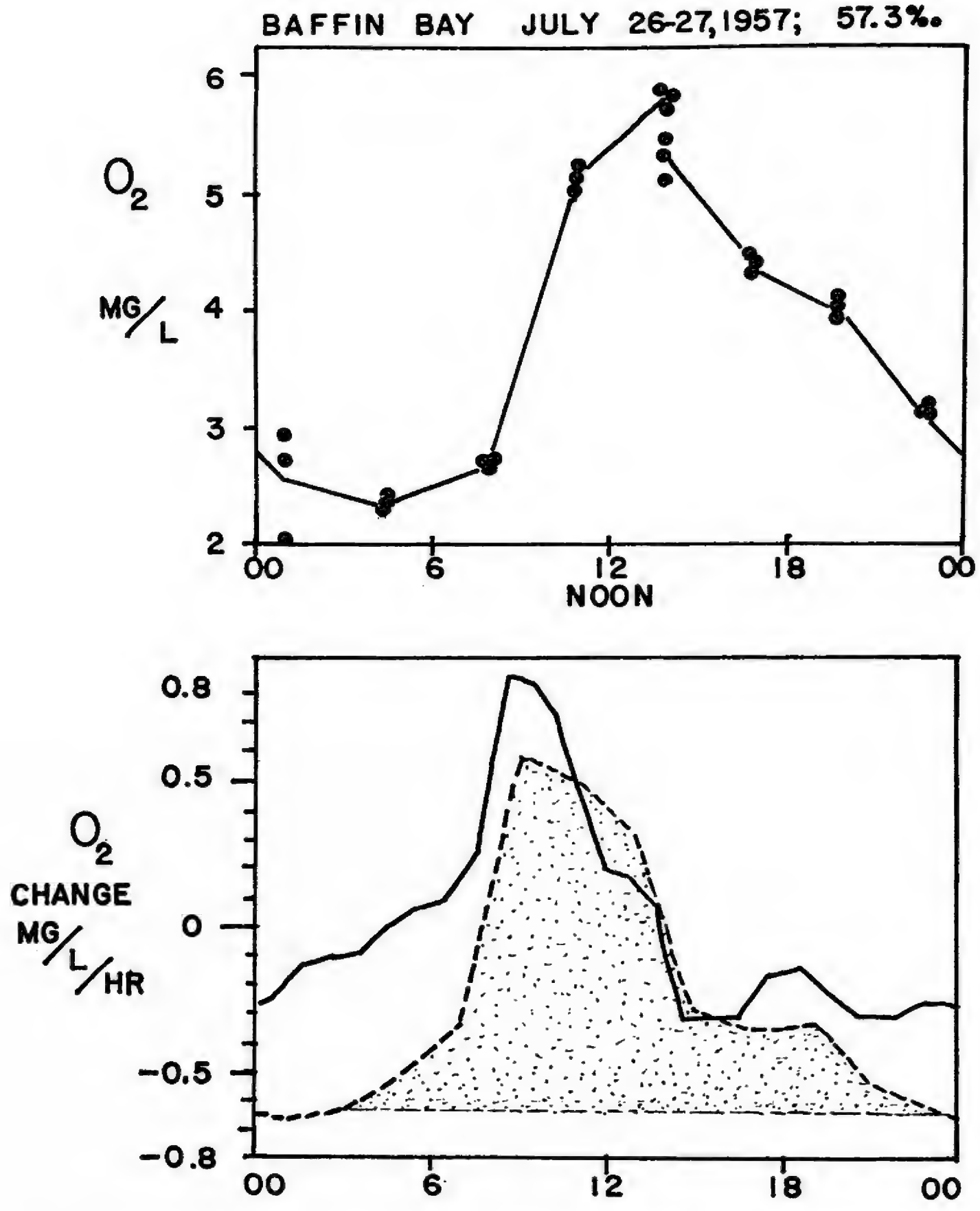


FIG. 4. Example of a diurnal oxygen curve with somewhat irregular night respiration line. Baffin Bay, July 26–27, 1957, a turbid, hypersaline bay. The dashed line in the lower graph has been corrected for diffusion.

bottomed, the error in estimation of the depth of the water in its flow is likely to exceed errors in the diurnal curve measurements themselves.

A few of the curves have irregular rate of change curves at night clearly associated with variations in wind velocity recorded by the observer in the field. A decrease in wind velocity, for example, just before dawn in Figure 6 decreased the diffusion coefficient. In general some smoothing of the night curve by averaging points is required where some basis for interpreting irregular points exists.

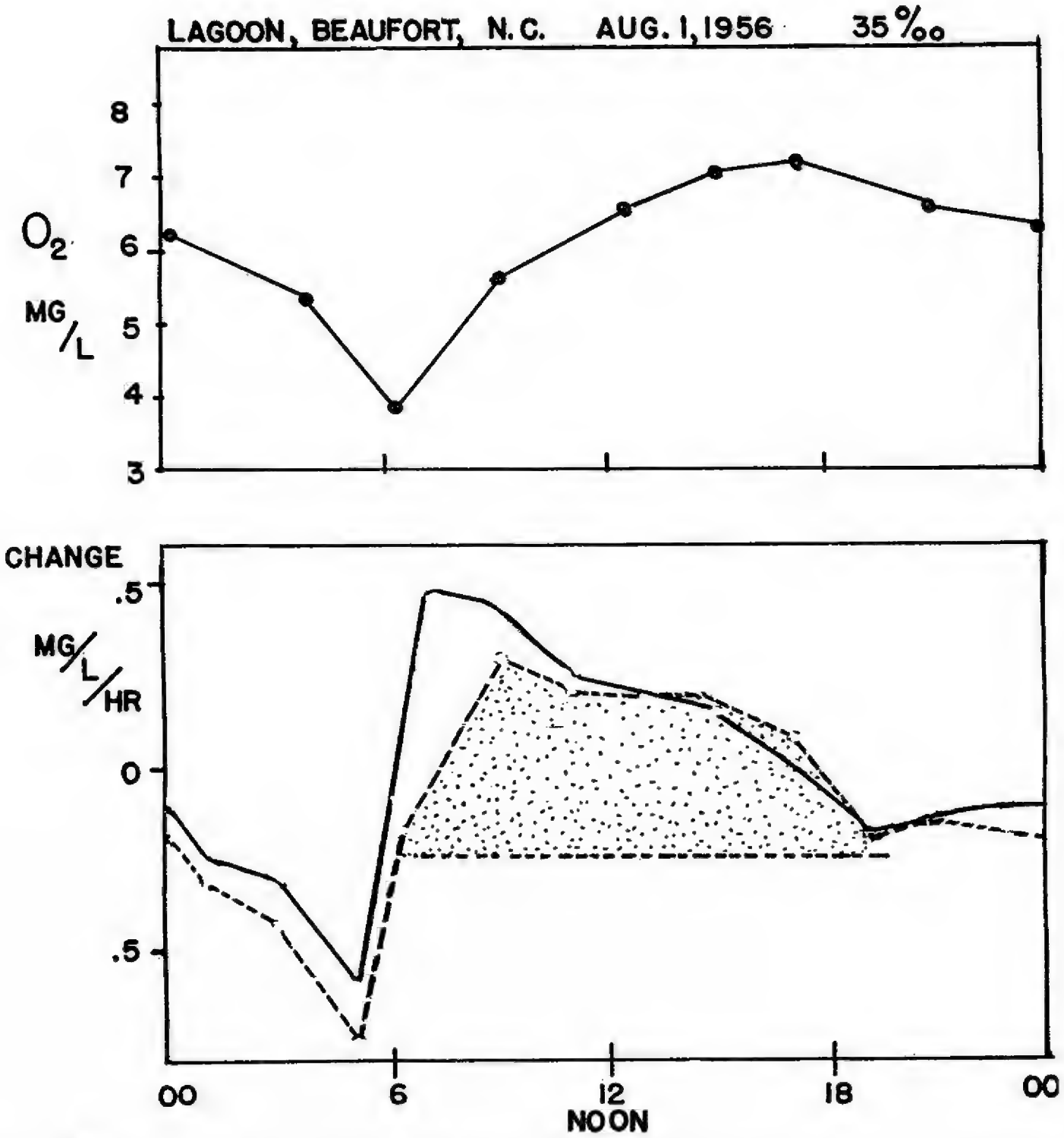


FIG. 5. Example of a diurnal curve for a terminal bay area in a tidal marsh system, Prytherch's lagoon, Beaufort, N. C., Aug. 1, 1956. The dashed line has been corrected for diffusion.

The separation of components of the diurnal curve such as given in this procedure and in variations previously described have been elaborately and formally expressed mathematically by Sugiura (1953, 1956). Although his results are similar, the math is not necessary for empirically established functions, which can be better understood with graphical work.

DIURNAL CURVE METHOD IN ESTUARIES

Experience shows that the diurnal curve methods cannot be applied in all estuarine water. A basic assumption of the free water methods is that analyses are made in water generally representative of the designated community area or water body. With the irregular flow systems usually found in estuaries, great care must be used in selecting suitable stations. Velocity is also important. A somewhat uniform diffusion constant must be assumed day and night. Since diffusion constants depend on current velocity, current variation introduces error.

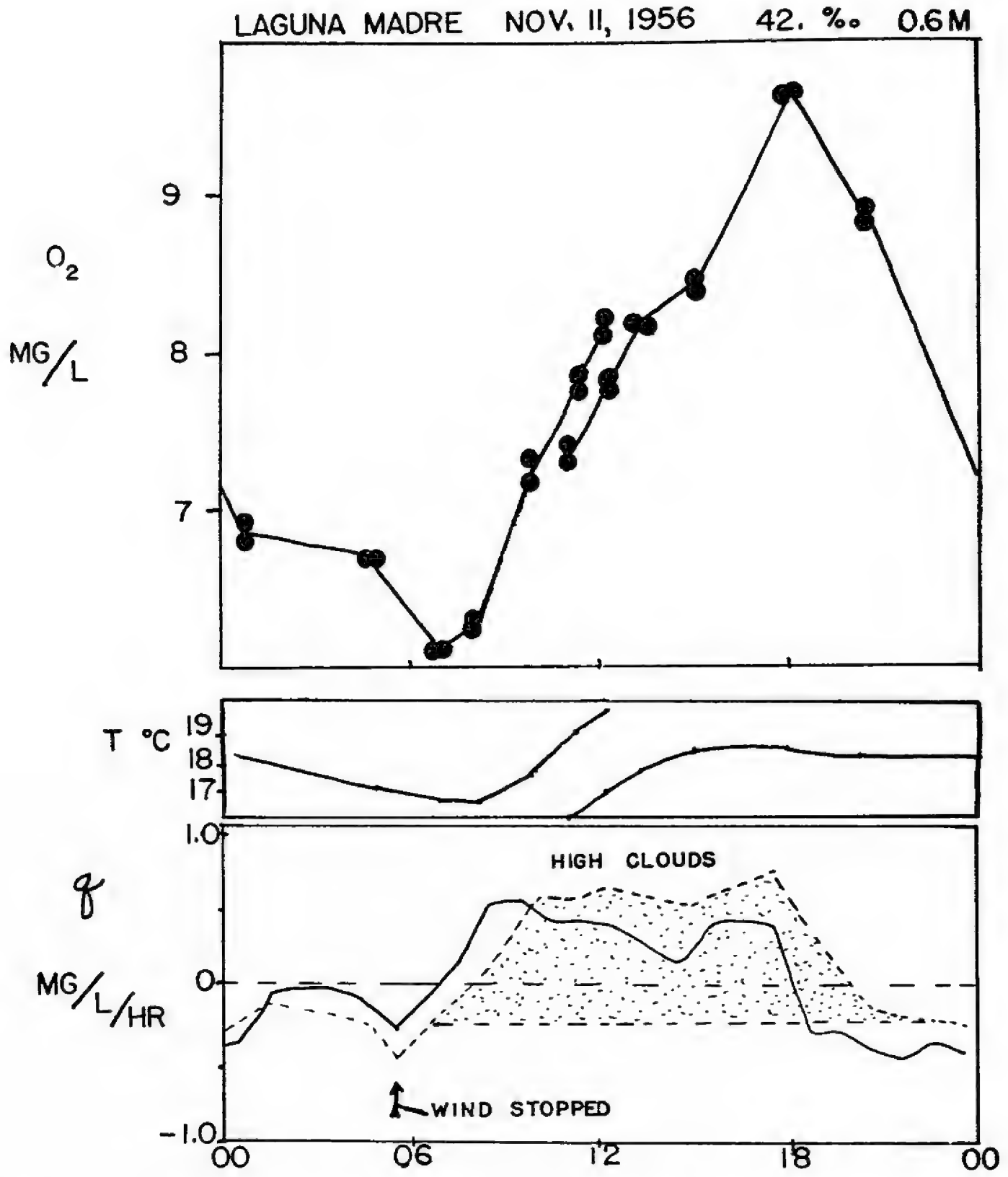


FIG. 6. A diurnal curve in which a cessation of wind was noted before dawn accompanied by diminished diffusion and momentarily increased rate of oxygen decrease (see arrow). Upper Laguna Madre, Red's Fish Camp, Nov. 11–12, 1956.

To test for suitability of the diurnal curve in a bay, duplicate and simultaneous measurements should be made at several stations. If there is no great range of values, the data at each hour may be safely lumped and the computation applied to the whole curve. In Figure 3 are similar data from 3 stations in one bay area.

When there is a slow drift over very fertile communities, dye markers may be applied and upstream-downstream measurements can be made as on reefs or the Florida Keys turtle grass (Odum, 1957b).

Where there is a strong tidal system as at Beaufort, N. C., the method cannot be used in the open bays or in channels. The heterogeneity of current velocity causes large differences in water mass, diffusion exchange with the atmosphere, and such large movements

of water that no water mass may be followed with practicality. In such flows current markers mark streamlines rather than trajectories. With this kind of mixing, trajectories of objects larger than colloidal size are a fiction as far as indicating water movement. Attempts to measure diurnal curves at the Institute of Fisheries of the University of North Carolina, Morehead City, in Bogue Sound yielded only saturation data for oxygen even though considerable metabolism was known to exist. Diffusion rates were very large.

It was hoped that narrow uniform tidal canals were sufficiently uniform that a diurnal curve at one station would indicate a general metabolism. Such a curve is shown in Figure 7 for Core Creek, near Beaufort, N. C. Times of maximum tidal current are indicated. It is clear from the graph, however, that rates of diffusion were varying tremendously, being large during strong flow and diminishing during lesser flow. At times of strong current (arrows in Fig. 7), oxygen concentrations returned towards saturation. Fortunately, it is easy to recognize some complication when the diurnal curves have unusual shape.

The diurnal curve can be used as an approximation however, in a tidal estuary if one selects a partially enclosed terminal body in which the water has minimal motion. A curve for such a body in Beaufort, N. C. is given in Figure 5. During the 24 hour period only part of the water moved gently out and gently back. The extent to which the history of the water returning differed from the water leaving is the extent of the error.

Fortunately for workers in the bays of Texas, tides are small (0.3–0.6 M/day) in the Gulf and mostly damped out in the bays. Fresh water flows and winds dominate circulation. If one picks a 24 hour series in one wind regime, conditions are ideal with enough mixing to prevent stratification but usually with not enough water current velocity to make diffusion corrections large. Since all of the Texas bays are only 1 to 12 ft. in depth, bottle measurements are of little use for total metabolism and the diurnal curve method is the only method now possible. See comparison of bottle and diurnal curve methods that follows.

In the lagoon at Bimini, British West Indies the water enters with the tide from two sides. By choosing a station in the area where the flows meet, an area of minimal current was found for obtaining a diurnal curve (Fig. 8). The data from this shallow area represent the water that for the most part is being modified by the hard, algal covered, limestone substrates in the wide central area.

Inverted Curves

Among the situations which are easily recognized as unsuited for usual production and respiration measurements are the inverted curves in which oxygen is observed to increase during the first part of the night and to decrease during the day. One such curve was found on a dystrophic swamp river in coastal North Carolina (Fig. 9). Measurements with a thermistor during the day indicated temperature stratification in the top layer of the opaque brown water. A suggested interpretation of the inverted diurnal curve follows. The large respiration of the particulate and dissolved swamp materials far exceeded photosynthesis. A balance between respiration and diffusion from the air existed during the night but was interrupted during the day by the temporary temperature stratification which cut down the diffusion constant so that oxygen removed by respiration could not be renewed as rapidly as after nightfall. A similar curve was found

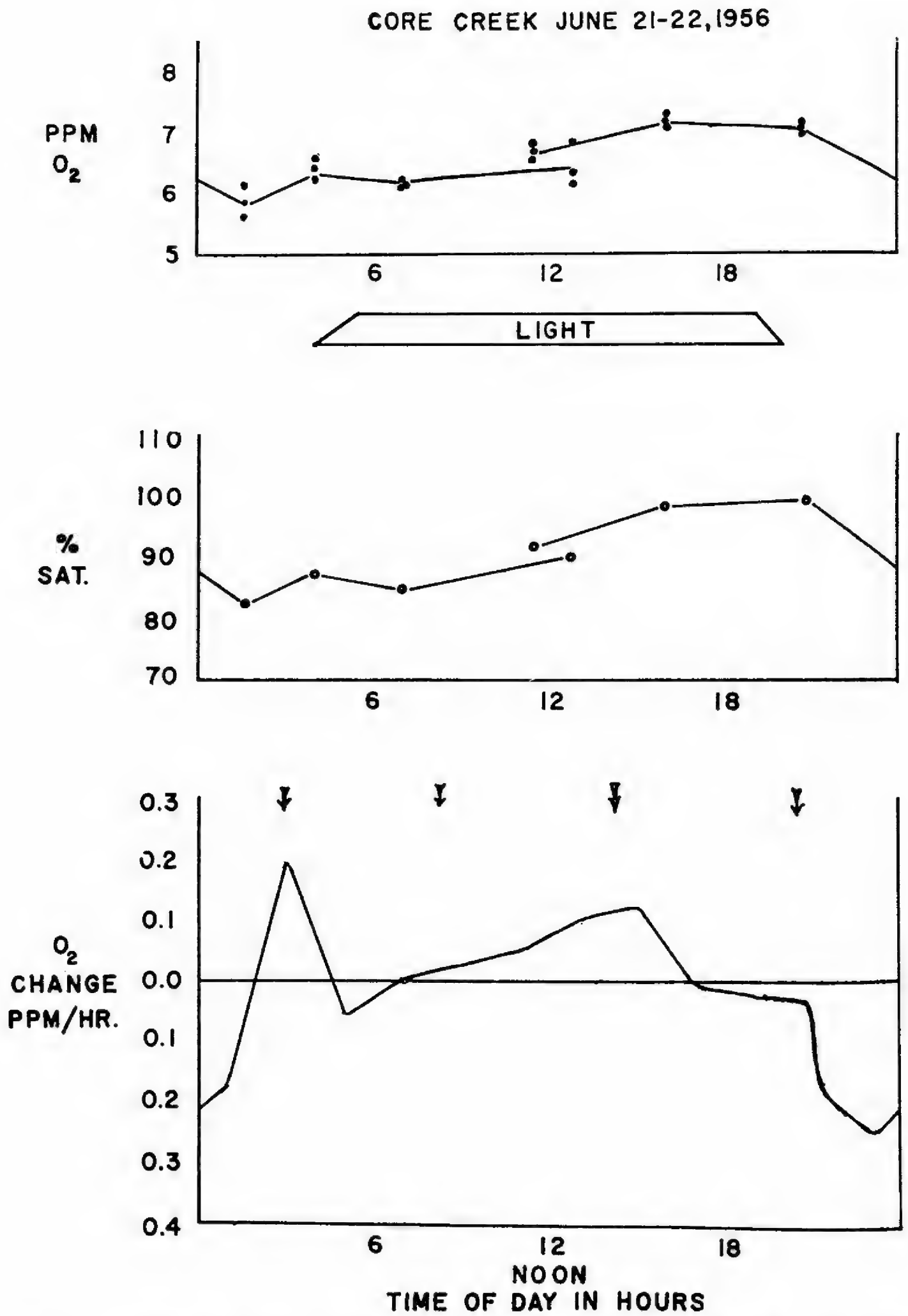


FIG. 7. A diurnal oxygen curve in a narrow tidal canal between two large bays, Core Creek, Beaufort, N. C., June 21–22, 1956. Current velocities range 0–4 knots during the period. Metabolism can not be computed from this curve with accuracy. Arrows indicate times of maximum current velocity.

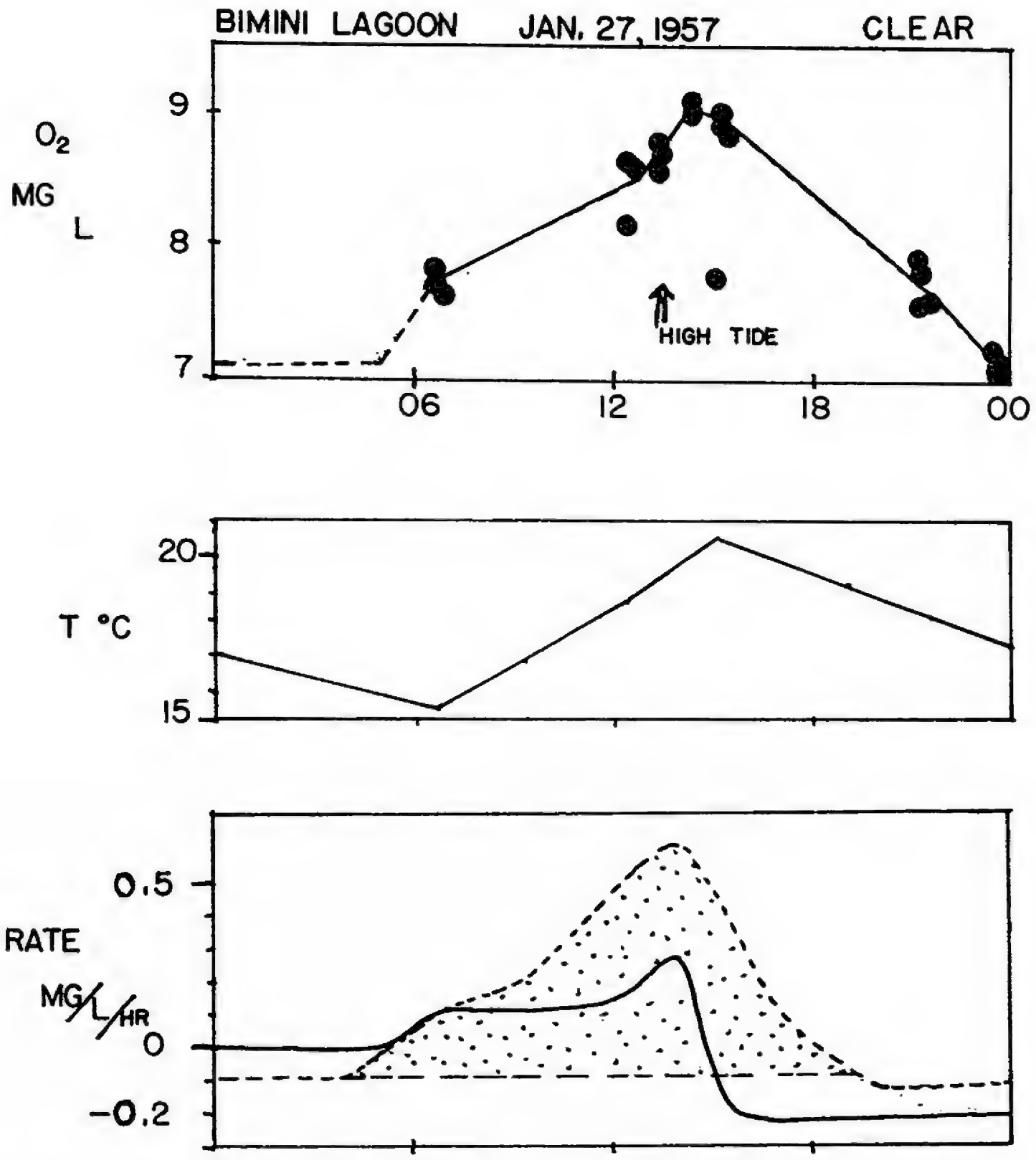


FIG. 8. Diurnal oxygen in a minimal current area in an area of convergence-divergence of Bimini Lagoon, Bimini, British West Indies, January 27, 1957. Data in cooperation with Dr. Louis Kornicker with courtesy of the Lerner Laboratory and the American Museum of Natural History. Substrate is an irregular limestone with algae, turtle grass, and benthic animals.

by Laurie (1942) and by Hoskin in Singletary Lake, N.C.; another opaque, dystrophic body strongly colored with swamp seepages.

DIURNAL MEASUREMENT FROM AN OFFSHORE OIL DRILLING PLATFORM

It has been previously assumed that diffusion is so rapid that the diurnal curve methods are impractical in deep and relatively poor waters of the open seas. However, one can never eliminate diurnal changes in oxygen entirely because the rate of diffusion is proportional to the saturation deficit. As the deficit becomes small, so does the diffusion rate. Sugiura (1953, 1956) was successful in determining diurnal oxygen changes in open waters of Japan.

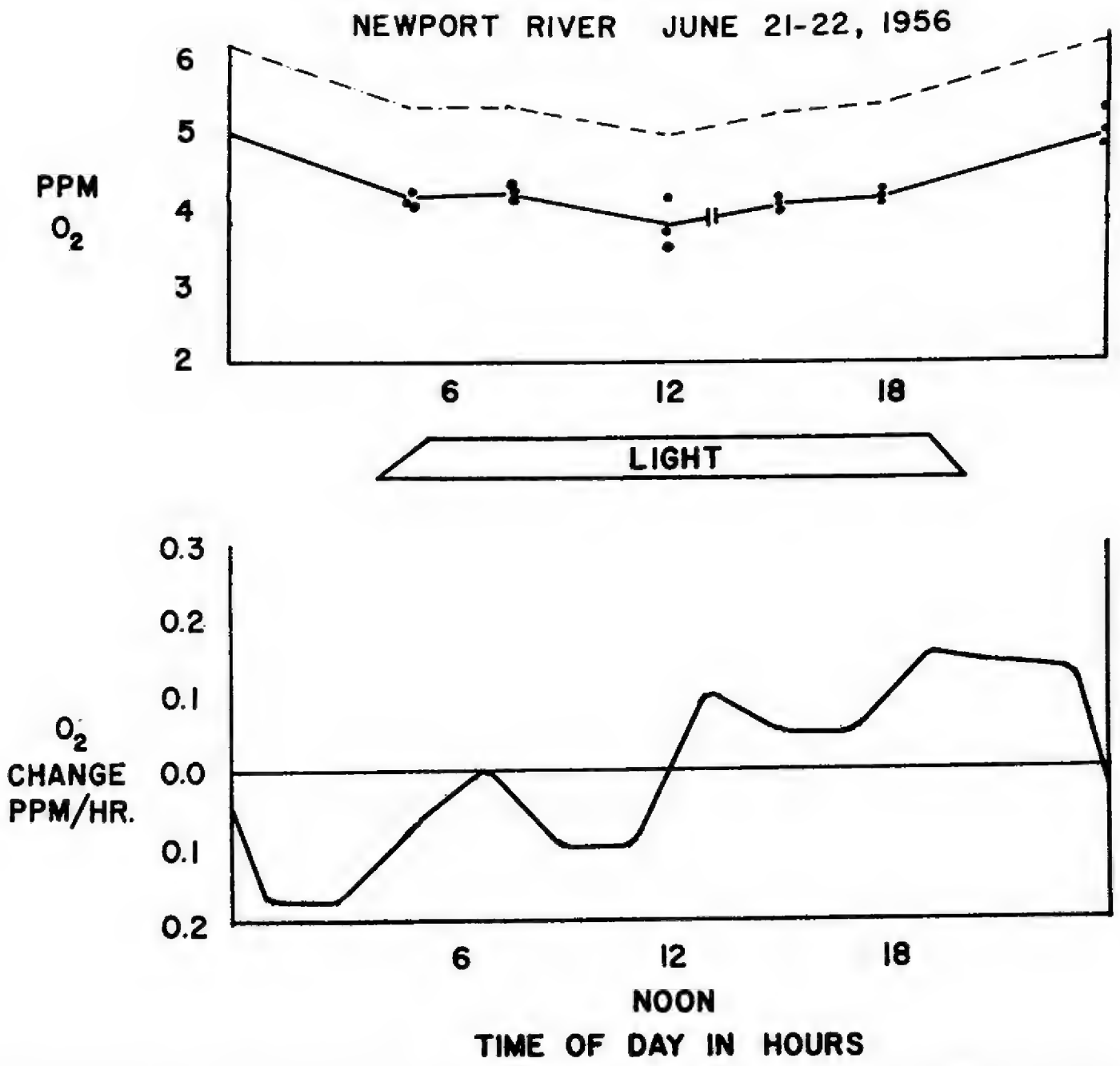
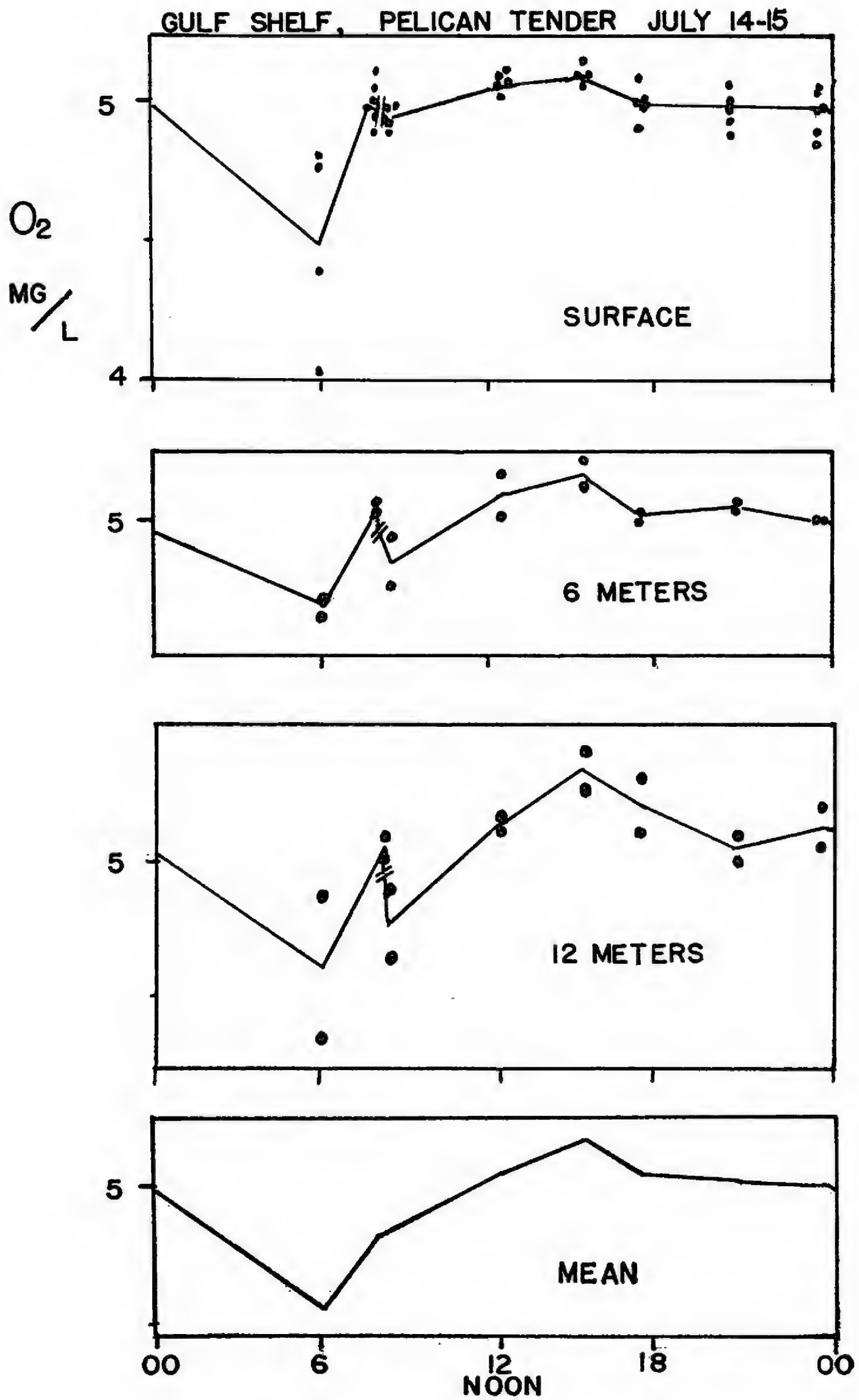


FIG. 9. Diurnal oxygen curve of inverted type in a brown dystrophic swamp river (200 ppm color), Newport River, Beaufort, N. C., June 21–22, 1956. Changing rates of diffusion and changing rates of respiration during the day produce a curve which cannot with present understanding be converted into metabolic figures. The dashed line in the upper curve represents correction from the Ohle test for interference.

The possibility of determining metabolism of the Texas shelf waters from oil rig towers was investigated near Port Aransas. Accuracy was increased by obtaining a large number of duplicate samples for the Winkler analyses as plotted in Figure 10. There seems to be no doubt that a diurnal curve was observed during a gentle 1 M wave swell in 15 M of blue Gulf water. The strong coastal current running from the south during most of the period stopped in the period before 6 A.M., and the accumulations of fishes and the garbage of the rig may have affected metabolism in a local atypical manner. Even if this one time of day is ignored, a production value may be computed. The diurnal changes in the lower part of the water column were greater than at the surface. The bottom occurs within the euphotic zone in the clear blue water and maximum metabolism may have been in lower levels. Diffusion from above may also explain the smaller daily amplitude of the surface data. The free water calculation indicated greater photosynthesis than in concurrent bottle experiments. There is a possibility that metabolic

FIG. 10. Diurnal oxygen curves at 3 levels in blue Gulf of Mexico water beneath an oil drilling tower, July 14–15, 1957.


GULF SHELF, PELICAN TENDER JULY 14-15
O_2
MG/L
5
4
SURFACE
5
6 METERS
5
12 METERS
5
MEAN
00
6
12
NOON
18
00

estimates with bottles are too low even in shelf waers. A discussion of the use of bottles follows.

Light and Dark Oxygen Bottle Methods in Estuaries

The light and dark bottle methods have now had wide use in limnology and oceanography, but some care with the details of their use has been found essential for obtaining reproducible results in estuarine waters as follows:

Replicate oxygen samples in the free water normally indicate great heterogeneity of oxygen and populations. Thus plankton water used for filling start, light, and dark bottles must be homogenized in order to reduce variability. This is done by filling a 5 gallon carbuoy with bay water and swirling it for 5 minutes. Then this water is siphoned into 250 cc BOD (biochemical oxygen demand) bottles and filled in order: one start bottle, one light bottle, one dark bottle, etc. so that any bias in sequence of filling is dispersed uniformly among replications. Three replications of each category are considered necessary.

Aluminum foil as a cover for black bottles is unsatisfactory because as crinkles develop, pinholes permit light to enter. Aluminum foil also reacts rapidly with salt water. Black, taped bottles are suitable with rubberized black cloth wrapped around and fastened with a heavy inner tube rubber band.

When these precautions are taken, duplicate starting bottles are usually reproducible within 0.2 mg/1. After chemical fixation precaution in mixing the 250 cc bottles containing iodine is necessary prior to titration. It is believed that the distribution of iodine is affected by silt particles which settle to the bottom.

In all oxygen analyses the direct Winkler process is usually adequate for non-polluted estuaries. The Ohle (1953) procedure was used for testing for Winkler interference. In all cases reported here interference was small (less than 0.3 mg./1) and was ignored since the production and respiration measurements are based on diurnal differences. The actual value of the oxygen affects computations only in the calculation of the diffusion correction.

Table 1 is a sample data sheet. A similar sheet was made for each bottle metabolic rate computed. In deeper waters 3 light bottles were placed at each of three depths. In shallower waters (1 M) bottles were placed at two depths. It is essential that light bottles be placed in the optimum light zone as well as in layers above or below. Optimum light is about 1/5 daylight.

Table 1

Example of Data Sheet on Metabolism in Bottles.
Data are given in mg./L (Gm./M^3).
Laguna Madre, August 1–2, 1957, depth 0.46 M

Start	Dark	Light top	Light bottom
5.90	4.89	6.92	7.05
5.90	4.73	6.96	6.98
5.99	4.70	6.90	7.40
5.93	4.77	6.93	7.14
			7.03

$R = (5.93 - 4.77)\ (0.46\ M) = 0.53$ gm./M^2/day
$P_n = (7.03 - 5.93)\ (0.46\ M) = 0.51$ gm./M^2/day (net yield of the bottle system)
$P_g = P_n + R = 1.04$ gm./M^2/day (gross photosynthetic production of the plankton community)

Comparison of Diurnal Curve Methods with Bottle Measurements

In Table 2 are reported the results of diurnal curve measurements and bottle measurements made simultaneously at the same station. Data from tanks are reported along with

Table 2

Comparison Between Measurements of Metabolism made with Bottle Methods and Free Water Diurnal Curve Methods
P and R Data are in gm./M^2/day Oxygen. K is the Diffusion Constant in gm. O_2/M^2/hr. for 0 per cent Saturation as Computed from Diurnal Curve Data

	Bottle Method		Free Water		
	P	R	P	R	K
I. Systems without large bottom communities; plankton principally					
Fresh-water tank, stirred, pond water, Durham, N. C., May 25, 1956	1.50	0.83	1.16	3.30	0.49
Sea-water tank, open, Beaufort, N. C., June 20, 1956, stirred	2.40	0.73	1.90	1.61	0.67
Sea-water tank, plastic cover, Beaufort, N. C., June 27, 1956	1.17	1.58	1.10	1.61	0.08
Diatom bloom in marine creek, Ryther et al. (1958)	4.8	.....	5.4	.....	.....
II. Systems with both plankton and bottom mud components					
Stewart Farm Pond, Durham Co., N. C., March 10, 1956, stratified	1.12	1.26	2.18	2.10	0.10
March 29, 1956, stratified	1.63	0.79	4.52	5.24	0.11
Prytherch's Lagoon, Beaufort, N. C., Aug. 1, 1956; data of Duke Oceanography class	6.25	2.76	4.50	5.80	0.78
Baffin Bay, Riviera, Texas, July 26, 1957	1.90	7.91	2.70	14.1	0.92
Baffin Bay, Riviera, Texas, Dec. 23, 1957	3.0	4.0	3.7	5.0	1.3
Gulf shelf off Port Aransas, Pelican drilling tower, 15 M deep, July 14, 1957	2.0	9.4	6.7	7.5	.....
Tres Palacios Bay, June 17, 1957, salinity 2.4‰, turbid	4.3	1.1	6.4	10.2	1.4
Lavaca Bay, lift bridge, June 17, 1957, salinity 4.8‰, turbid	1.53	1.50	.....	.....	.....
Cedar Bayou, July 22, 1957, salinity 24.6‰, 1.5 M deep	2.5	2.1	5.6	17.6	1.5
Mesquite Bay, July 22, 1957, salinity 15.5‰, Algal bottom, 1.2 M deep	0.85	0.95	3.8	7.3	1.2
Mesquite Bay, July 22, 1957, salinity 15.5‰, Shell bottom, 1.1 M deep	0.75	0.86	1.2	3.6	0.4
Copano Bay, May 18, 1957, Rt. 35 bridge, 1 M deep, salinity 13.1‰	.....	.....	23.8	13.7	3.8
Bayside, salinity 29.9‰	.....	.....	8.0	8.5	1.8
Copano Bay, Aug. 8, 1957; salinity 11.8‰	1.86	2.3	2.1	6.2	0.7
Copano Bay, Oct. 20, 1957	0.26	0.44	1.60	1.65	.....
Aransas Bay, Rockport Pier, May 19, 1957, 1 M deep, salinity 21.0‰	.....	.....	6.3	4.8	0.6
Oct. 20, 1957, 1.3 M deep, salinity 18.7‰	0.59	1.1	6.1	7.8	1.8
Rockport Harbor, Aug. 5, 1957, salinity 34‰, after a bloom	.....	.....	6.1	11.6	0.8
Corpus Christi Bay, Ingleside, June 21, 1957, salinity 22.9‰	2.3	1.5	9.4	11.8	1.1
Overflow tidal pool, South Jetty, Port Aransas, 0.15 M deep, July 1, 1957	0.96	0.24	1.48	3.7	0.4
Flood Pool, Ferry Road, Port Aransas 0.9 M deep	2.4	1.01	5.2	11.7	1.4
III. Systems with dominant bottom plant and animal communities; plankton unimportant					
Laguna Madre, Texas, Mean, *Diplanthera*-ooze, 1957, Annual Curve (Figure 10)	0.70	0.29	4.3	5.6	0.2–1.4
Redfish Bay, Port Aransas, Texas, *Thalassia* beds; Ransom Island, Mean of 5 days in all seasons	0.12	0.20	11.4	17.0	0.6–1.7
Bimini Lagoon, British West Indies, Limestone Flats, 0.3–0.6 M depth, (Fig. 8)	0.36	0.31	2.8	1.8	0.75

data from natural waters. All rates are reported in grams of oxygen per hour per square meter of community surface area.

The bottles represent plankton metabolism only, whereas the diurnal free water measments include effects due to the metabolism of the bottom and lateral surfaces. In the farm pond, the water was partially stratified, and oxygen at three levels was measured and multiplied by the pond volume at this depth based on a hypsographic curve of depth and area. In shallow bay waters steady stirring due to waves was observed and mixing was confirmed with fluorescein dye. Samples at several depths were similar in oxygen content indicating that mixing had been effective.

In group I in Table 2 in freshly filled tanks where bottom communities are minimal, there is order of magnitude similarity of free water and bottle measurements.

In Group II in Table 2 in the farm pond and shallow mud bottom bays, the respiration values are consistently much larger in the free water method probably because of the respiration of the mud surface and larger swimming animals included in the free water measurements. In environments of Group II where most of the photosynthetic production is planktonic (not benthic) it is not surprising that there is some similar order of magnitude in bottle and free water measurements of photosynthesis.

It is clear from the data on the shallow mud bottom systems that no adequate estimate of respiration or community BOD can possibly be obtained from bottle measurements. In this respect the bays and ponds resemble the streams where bottom respiration predominates (Odum, 1956; Hoskin, 1957). Such conclusions must apply to any bottle measurements including radioactive carbon measurements. One is forced to suspect studies like that of San Diego Harbor based on bottles (Nusbaum and Miller, 1952). Only in deep water or bloom situations where the bottom role in respiration is relatively minor, can bottle measurements in shallow water indicate community metabolism.

When bays are sufficiently shallow or clear enough so that appreciable light reaches the bottom, benthic plant communities develop lush communities. In such cases (Group III, Table 2) as Redfish Bay near Port Aransas, the bottle measurements of both photosynthesis and respiration are completely unrepresentative of the whole community being one hundred times too small. Because bottom metabolism can be so important in bays 3 meters deep or less, discussions of nutrient cycles are incomplete if made on the basis of plankton alone as in Great Pond, Mass. (Hulbert, 1957).

Although the bottle methods are not suitable in marine bays for total metabolism, they are apparently very useful in determining that part of the metabolism which is due to plankton. For this purpose, bottle measurements were continued in subsequent measurements in Texas Bays.

Even where bottom metabolism is not a factor, free water measurements are likely to be superior to bottle measurements especially where diffusion corrections are small or known accurately. In bottles the normal turbulence is eliminated as well as the continuous flux of water from regenerative parts of the system bringing nutrients. The constant level of a bottle suspended on a post or buoy does not provide the varying light conditions characteristic of nature. The rapid deterioration of metabolism in bottles has been shown by Ichimura and Saijo (1958) with radio-carbon methods. However, other evidence (Verduin, 1957) indicates there are disadvantages of very short time measurements before cells become somewhat adapted to new conditions. The rapid modifications of bottle communities have been much studied especially relative to the changing role of bacteria (Vaccaro and Ryther, 1954). Whether the increased accuracy

of a larger change in a longer period outweighs advantages of small population changes during shorter time is not known. Experience with lags and shocks in bell jar work (Odum, 1957a) as well as plant physiological work suggests that very short periods of a few hours may be imperfect. Most of the bottle measurements in this study were for 24 hour periods because of logistic requirements.

Bell Jars and Mud Bottles

Whereas the diurnal curve method provides estimates of metabolism of the plankton, nekton, and the bottom mud, the role of the bottom mud algae is determined wtih difficulty. Bell jars have been used previously over grass and reef substrates by Odum and Odum (1955), Odum (1957a), and Odum, McConnell, and Abbott (1958). As previously discussed such measurements are very rough because of technical difficulties and because the rate of circulation of water is a controlling factor in benthic metabolism (Odum, and Hoskin, 1957). Some additional measurements of bell jar metabolism

Table 3

Oxygen Metabolism Measurements in Shallow Texas Bays; Comparison of Bell Jar Methods with Bottle and Free Water Methods

P, gross photosynthesis; R, total respiration; P and R data are in gm./M^2/day oxygen. K is the diffusion constant in gm. O_2/M^2/hr. for 0 per cent saturation as computed from diurnal curve data.

	Bottles		Bell Jars		Free Water		
	P	R	P	R	P	R	K
Laguna Madre, Reds camp, Nov. 11–12, 1956	....	.....	2.1	2.1	5.1	3.2	1.4
Jan. 21–22, 1957	0.31	0.18	0.34	0.19	3.8	7.2	1.4
March 27, 1958, (by W. McConnell)	0.30	0.27	1.40	2.7	3.8	3.8	0.4
Redfish Bay, Ransom Island, Jan. 31, 1957	0.17	0.25	1.1	0.7	5.1	7.5	0.7
Baffin Bay, Riviera, Feb. 4, 1957	2.7	1.3	0.95	0.36	16.6	9.6	3.4
Bluegreen Algal Mat, 0.15 M deep, Portland, Texas, McConnell and Odum, May 26, 1958	.....	.....	1.3	1.0	2.2	1.9	0.3

over estuarine bottoms were made in Table 3 for the Texas bays. The bell jar measurements are consistently too low in both photosynthetic and respiratory metabolism as compared with the free water measurements. From evidence so far available, bell jars are good only for order of magnitudes and inferior where free water methods are available.

Another method involves measuring the metabolism of a mud surface which is allowed to develop in a 250 cc BOD bottle. A suspension of representative bottom mud is introduced into the bottle and a one inch layer is allowed to settle. Then the excess water is gently siphoned off and replaced with water from a carbuoy of known oxygen content. After 3 hours part of the water sample above the mud is gently siphoned off into a small oxygen bottle where Winkler analysis can be carried out. As indicated in Table 4 an estimate of the respiratory metabolism per area of mud can be obtained in this way. Tests for interference with Winkler analyses due to diffusing substances from the mud into the free water indicate some effect. Thus such measurements are very rough, but they do indicate a large mud metabolism consistent with the high metabolic values ob-

TABLE 4

Dark Bottle Measurements in Estuaries; Comparison of the Respiration Rates of Stratified Mud Bottles with Plankton

All data expressed as gm. oxygen/M^2/day. Data from Oceanography Class, Duke University with Mary L. Sparling and Edward McCoy

	Plankton Dark Bottles	Dark Mud Bottles	Total
Beaufort estuaries, N. C., 2–3 M deep.			
July 8, 1956	4.85	1.02	5.87[a]
July 15, 1956	2.55	1.52	4.07[a]
Aug. 20, 1956	0.55	2.64	3.19[a]
Aug. 1, 1956	2.76	.....	5.80[b]

[a] Sum of plankton and mud bottle estimates on an area of community basis.
[b] Free water diurnal curve method used for total metabolism.

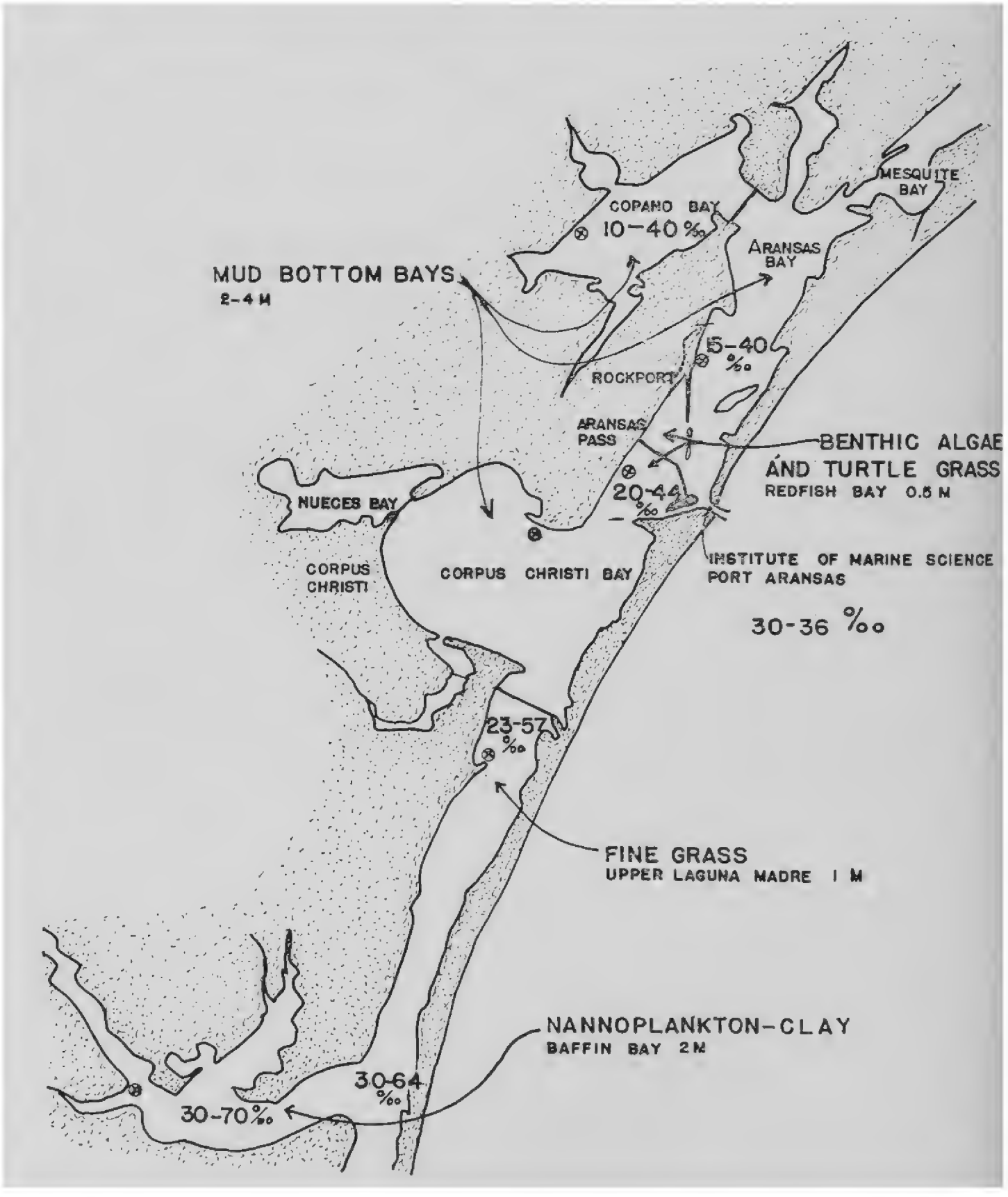


FIG. 11. Map of marine waters in the vicinity of the Institute of Marine Science, Port Aransas Texas. Numbers are salinities during the period of measurement of this paper.

tained with the diurnal curve measurement in the free water. Whereas neither the bell jars nor the mud bottles provide desirable accuracy, no other way to check the mud metabolism estimates of the diurnal curve method has yet been worked out. The sum of respiration of plankton and mud bottles is sufficiently large (Table 4) to confirm the important role of the bottom as indicated by the diurnal curve estimate of metabolism.

Community Metabolism

Comparison of Metabolic Rates in Texas Bays

Measurements of gross production, community metabolism, plankton production, and plankton respiration were made in several seasons in the major Texas bays near Port Aransas as shown in Figure 11. The values for total metabolism computed from the diurnal graphs and from the dark-light bottle series are summarized in Table 2. The individual daily curves are not all reproduced, but each curve is based on 12 to 24 Winkler analyses. In most cases the corrected rate of change graphs have a hump shape like Figure 1, 2, 3, 4 and 6. In only two communities was a midday depression in total metabolism observed. These were communities with plankton blooms (Fig. 5 and Rockport Harbor, Aug. 5, 1957).

The shallow bays like Redfish Bay and the upper Laguna Madre are in general more productive than the deeper bays like Copano, Aransas, and Corpus Christi bays, (Figure 12). The shallow bays in general maintain greater clarity with a large proportion of the metabolism on the bottom as indicated by the larger diurnal curve values in Table 2 relative to the simultaneous bottle measurements. Maximum production was 24 gm./M^2/day in a spring bloom in Copano Bay, but the highest sustained production was 7–18 gm./M^2/day on the grass flats of Redfish Bay at a station where there is some influence of a treated sewage outfall. High as these figures are they are not as great as found in some clear, well circulated turtle grass at Long Key, Florida with 34 gm./M^2/day (Odum, 1957b), at a coral reef at Eniwetok with 24 gm./M^2/day, in Silver Springs in May with 30 gm./M^2/day, or in polluted streams of order of magnitude of 60 gm./M^2/day (See review Odum, 1956). In the deeper and turbid bays, it is obvious that much of the available light is being absorbed by clay particles and is not reaching plant cells. The distribution of turbidity and turbulent stirring of the bottom oozes is a major factor in reducing potential productivity of Texas bays. There are possibilities for increasing productivity with procedures for clearing Texas bays.

On any one day there may be a considerable excess of either production or respiration (Table 2 and Fig. 12) but there is no independent evidence yet to indicate that the bays are regions of export, storage, or organic matter import. At present the methods are not sufficiently accurate or the data replicated sufficiently in any one bay to determine if the community has an annual small net production or loss.

Largest variations (1 to 24 gm./M^2/day range) from one time to another were observed in those bays with plankton populations like Copano Bay, Baffin Bay, and Aransas Bay. As might be expected photosynthesis of blooms is far more irregular than photosynthesis by attached benthic plant communities. Even in Baffin Bay, benthic measurements equalled free water measurement on only one day (Fig. 12).

The salinities represented in Table 4 cover the tremendous range from fresh water to hypersaline conditions of 79 parts per thousand. During this 1956–58 period salinity variation in single bays has been sharp and drastic. The general ability of the plant communities to maintain a considerable continuous primary productivity reflects the

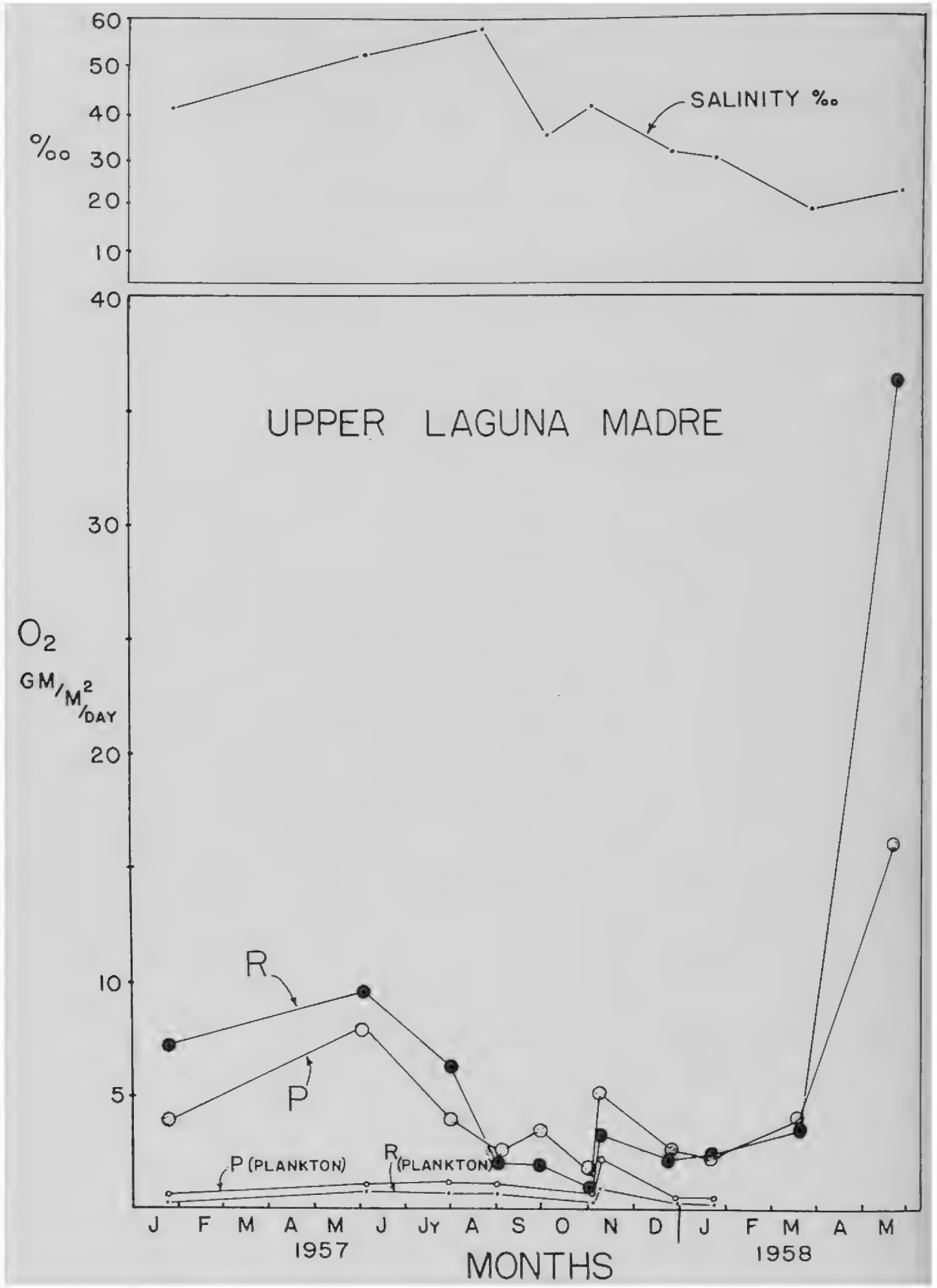
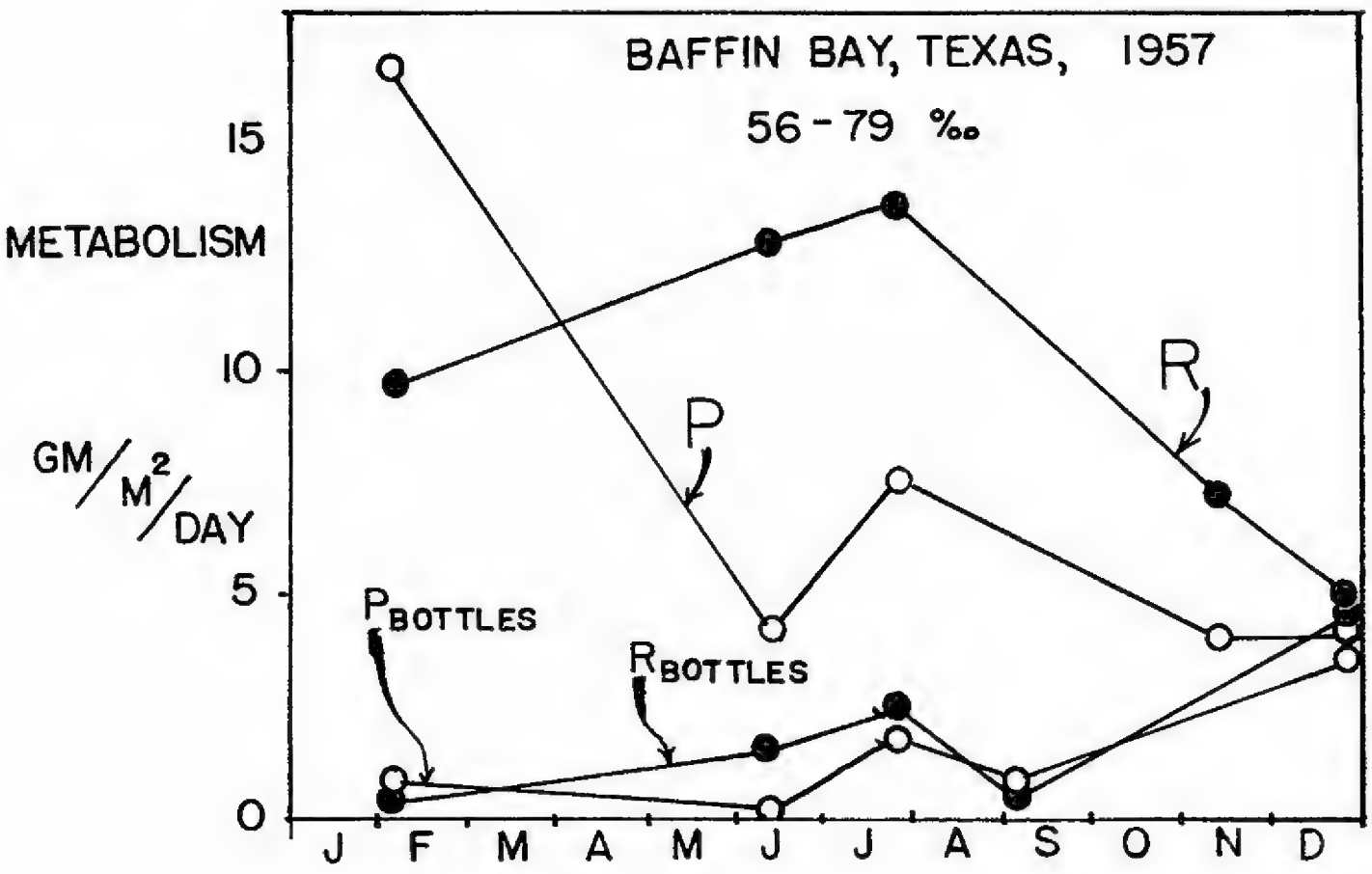


FIG. 12. For legend see next page.

rapid capacity of such communities to survive or recover in such estuaries. Neither high nor low salinity provides a limit to basic plant photosynthesis. Some of the highest production values were found in the extreme salinities in which many consumers are excluded physiologically.



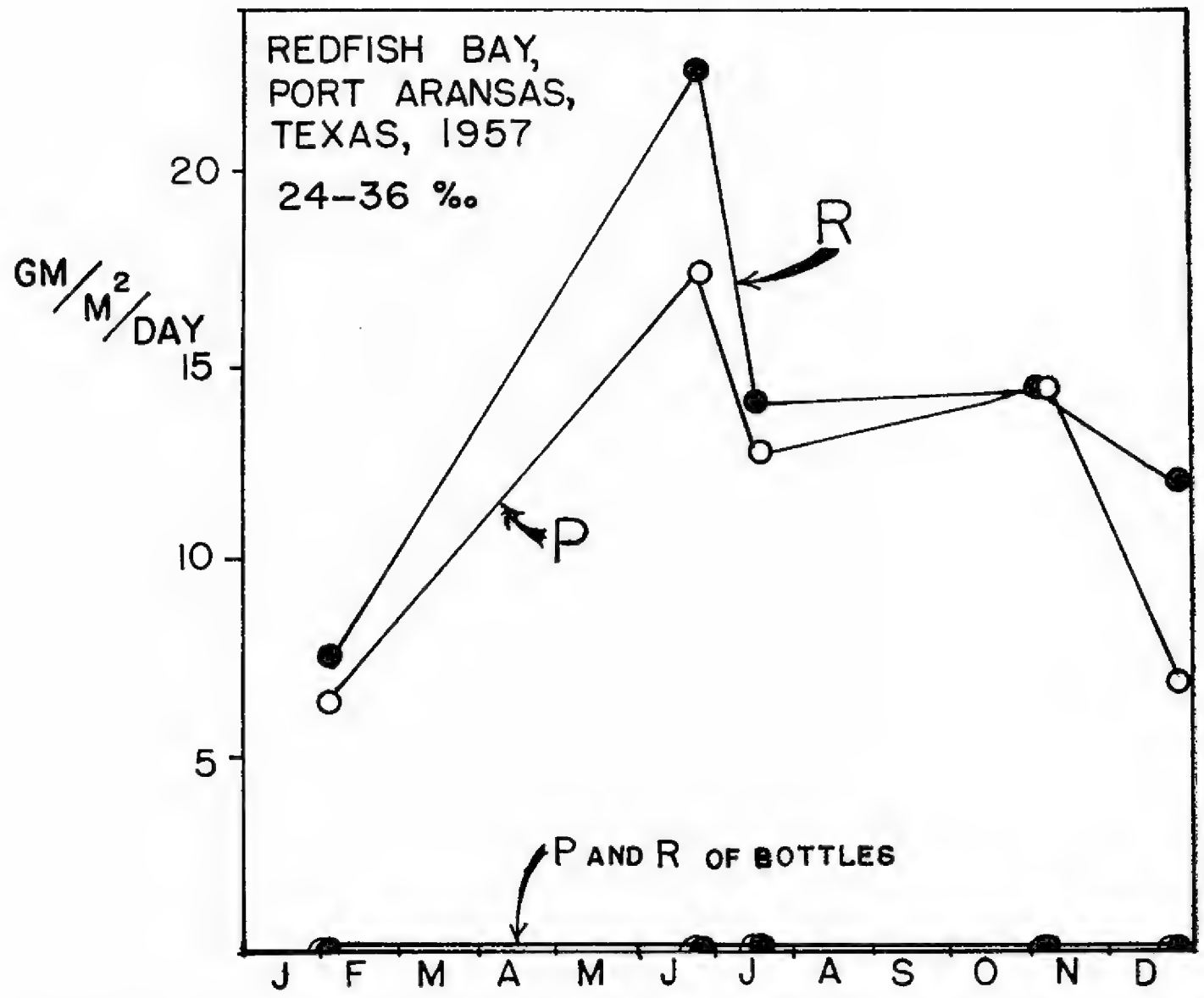


FIG. 12. Seasonal trend of metabolism in the shallow Upper Laguna Madre, Baffin Bay, and Redfish Bay. P, gross primary production; R, community respiration. The lower curves are dark and light bottle measurements; the upper curves are the result of diurnal curve measurements.

Seasonal Trend in the Grassy Upper Laguna Madre and Port Aransas Redfish Bay

In order to gain some annual picture in one area, metabolism measurements were made over a year's period in a representative shallow water area of the upper Laguna Madre. Data on both total metabolism and plankton metabolism are plotted in Figure 12. As found by Odum, McConnell, and Abbott (1958) with chlorophyll measurements, the producers include the plankton, the bottom algal ooze which often becomes suspended by wave action, and the fine bladed, sparse covering of *Diplanthera wrightii*. As the small values from bottles indicate, plankton metabolism is minor although small blooms occasionally occur as in November, 1957. (Fig. 12).

Maximum production as well as maximum respiration occurred in late spring or early summer in both years. There is also a well known development of consumer populations at this season due to the migration of larvae and rapid growth. Apparently these populations are closely geared to the gross community primary production although in any one day's measurement there is considerable range of the P/R ratio.

In winter the migration of many of the dominant consumers such as mullet and shrimp into the Gulf for breeding is correlated with the minimum availability of primary productive energy in the bays. Winter days are short and winter skies in Texas are markedly shaded by heavy cloud covers in many weeks.

A study by Mr. Tom Hellier, Jr. is in progress in cooperation with the Texas Game and Fish Commission to determine the relationship of fish growth to the primary production in the Laguna.

Diffusion Constants in Marine Waters with Suggestions for Computation of Pollution Capacity

One of the by-products of the diurnal curve calculation is the gas transfer constant indicating the rate of oxygen diffusion into or out of the bay waters per unit saturation deficit gradient. The diffusion constants are in Table 4. There is a remarkable uniformity of diffusion constant with values between 0.3 and 3.8 gm./M^2/hr at 0 per cent saturation. The values below 1 were observed on nearly windless days in shallow bays where bottom friction was large and flow minimal. The values of 2 or above occurred in the deeper bays under windy conditions. These values are similar to constants previously reported for streams and other mixing waters (See review; Odum, 1956).

The diffusion constant provides an estimate of the maximum excess of respiration over production which is permissible for a bay without conditions becoming anaerobic and producing fish kills. The diffusion of oxygen into a bay at the lethal oxygen content may be computed for a day by multiplying the diffusion constant per hour (K) by the saturation deficit (S) and by 24 hours. Oxygen added by photosynthesis is indicated by P. For a fish kill respiration (R) must be greater than $24KS + P$ where S is the saturation deficit considered lethal for desirable organisms. For example, in these bays K is usually about 1.0 gm./M^2/hr. at 0 per cent saturation or 24 gm./M^2/day. P is usually greater than 1.0 gm./M^2/day. If 10 per cent saturation ($S=90\%$) is lethal for fish, $24KS+P$ equals (24) (1.0) (0.9) + 1.0 or 22.6 gm./M^2 oxygen added per day. For a fish kill R must exceed 23 gm./M^2/day—a value well above usual values in Table 2. The only high rates of respiration were also accompanied by high rates of photosynthesis. Such

computations indicate the maximum capacity of a bay to accept organic pollution that does not also stimulate photosynthesis.

The capacity of Texas bay waters to reaerate by atmospheric diffusion is similar to that of moderate sized streams. It is markedly greater than the diffusion in enclosed stratified waters where diffusion is an order of magnitude less. The diurnal curve provides means for practical management of oxygen budgets in Texas bays.

Heterotrophic Fertility and the Use of Saturation Deficit to Classify Metabolism

It is possible very quickly and without calculation to recognize environments that are receiving organic matter in large quantities and metabolizing it in excess of their own photosynthetic production. If the percent saturation remains mostly below 100 per cent during the 24 hours, the community has more respiration than photosynthesis. cent most of the day (Fig. 13).

If the percent saturation curve is above 100 per cent much of the time during 24 hours, the community is making an excess of organic matter over its respiration. The saturation deficit can thus be used to recognize any extensive organic matter import whether it is organic pollution or organic matter from natural sources. The type of metabolism dominated by imported organic matter was termed heterotrophic in a classification system previously presented (Odum, 1956). However, small excesses of photosynthesis or respiration should not be considered as significant until some means for determining daytime respiration can be found.

The very turbid waters in the low salinity bays of Texas are receiving organic matter from the land along with the silts. The respiratory metabolism of such bays as Tres Palacios, Aransas, and Mesquite (Table 2) exceeds photosynthesis. The percent saturation curve of Tres Palacios Bay on June 17, 1957, for example, remains below 100 per cent most of the day (Fig. 13).

As Ohle (1956) has emphasized, communities of consumer organisms can be as abundant and a system just as fertile on organic imports as on its own production. The high values of respiration in some of the turbid Texas Bays suggest that there is at times as much consumer activity as in some of the more productive bays. It has long been thought that organisms such as the oysters that dominate the turbid bays can survive either on some kinds of algae or on some kinds of organic detritus. Menzel (1955) in his study of two species of oysters in the Texas bays near the Institute of Marine Science summarizes knowledge on oyster feeding without indicating the relative roles of live and dead foods in nature. The relative interchangeability of the two types of basic nutrition for consumers has yet to be adequately measured.

Daily Course of Efficiency of Photosynthesis

Diurnal rates of change provide an hour by hour chart of the photosynthesis of a community, which may be related to graphs of insolation in order to calculate efficiency. Considerable question has been raised as to the efficiency of photosynthesis at various times of the day (Pirson, 1957; Verduin, 1957). In Verduin's discussion of Silver Springs it was not recognized that oxygen curves in spring runs are the same as the oxygen rate of change curves (Odum, 1957a). Thus Verduin erroneously stated that morning efficiency was much greater than the afternoon efficiency in Silver Springs.

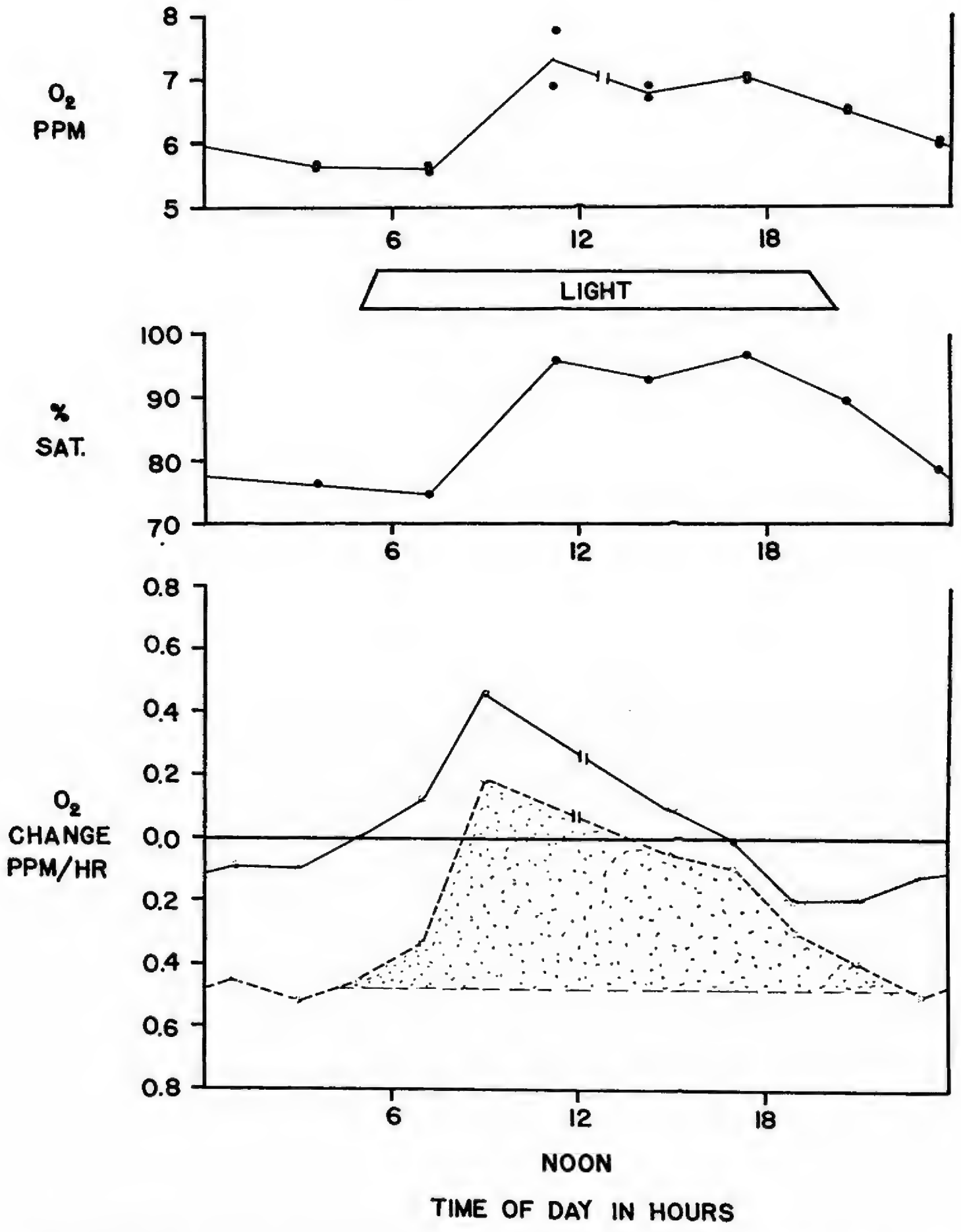


FIG. 13. A diurnal oxygen curve from a bay which is receiving more organic matter than it is producing. Note the percent saturation curve below 100 percent throughout the period. Trespalacios Bay, June 17–18, 1957. Data were obtained with aid of William Guest, Texas Game and Fish Commission. In the lower graph the dashed line has been corrected for diffusion.

Photosynthetic measurements are plotted as a function of light intensities in Figure 14 for one curve in Silver Springs and one typical curve for Redfish Bay. As might be ex-

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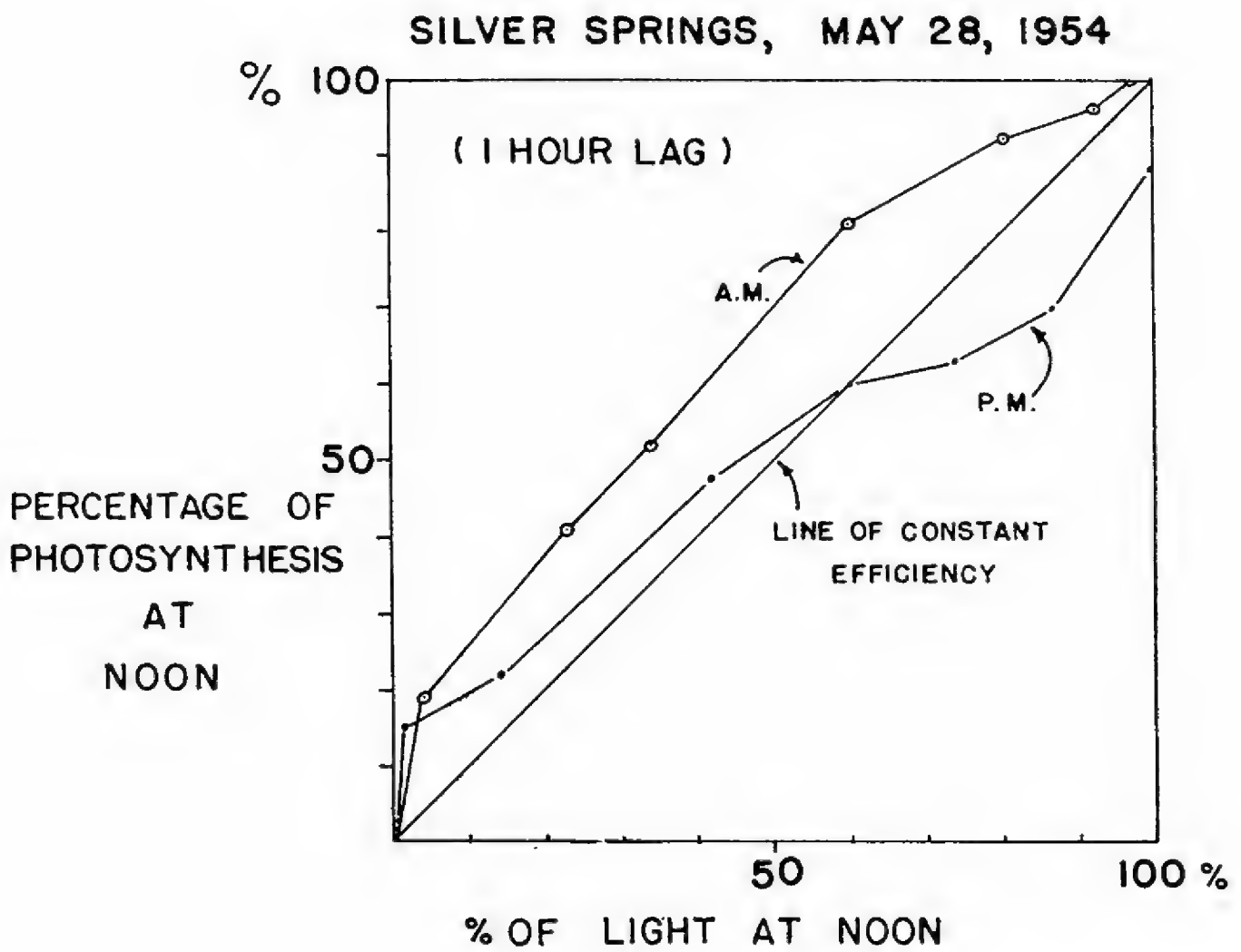
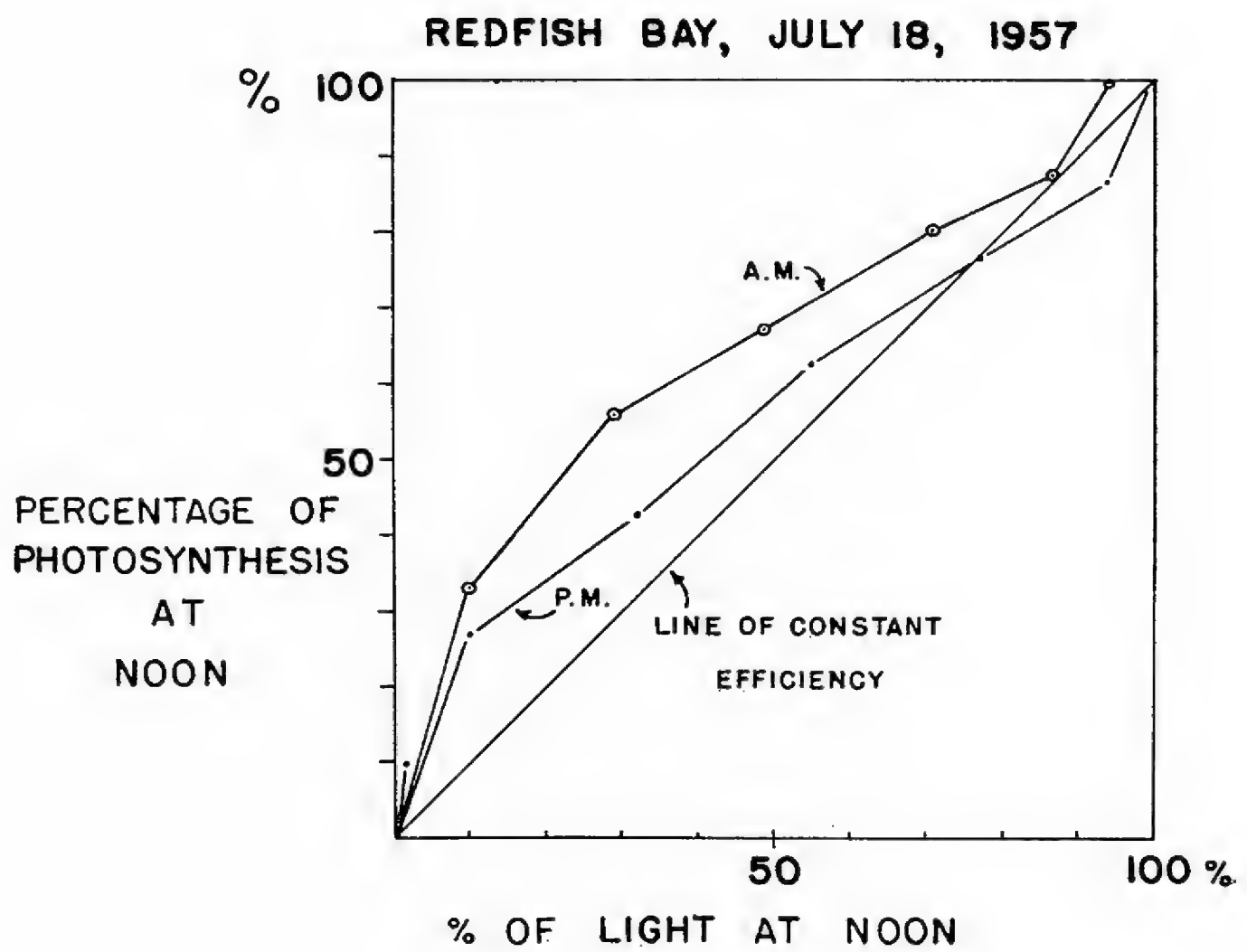
FIG. 14. Photosynthesis measurements of the whole community as a function of light intensity at various hours of the day. The upper curve is plotted from a diurnal curve for Silver Springs (Odum, 1957): The lower curve is from Redfish Bay, July 18, 1957. The diagonal straight lines are lines of constant efficiency for reference purposes.


SILVER SPRINGS, MAY 28, 1954
% 100
(1 HOUR LAG)
A.M.
P.M.
50
LINE OF CONSTANT
EFFICIENCY
PERCENTAGE OF
PHOTOSYNTHESIS
AT
NOON
50
100 %
% OF LIGHT AT NOON


REDFISH BAY, JULY 18, 1957
% 100
A.M.
P.M.
LINE OF CONSTANT
EFFICIENCY
50
PERCENTAGE OF
PHOTOSYNTHESIS
AT
NOON
50
100 %
% OF LIGHT AT NOON

pected from general behavior of plants in photosynthesis (Rabinowitch, 1951) efficiency is higher at low light intensities (early morning and evening) and declines as the power output increases in the middle of the day. In these curves there is only slight difference between morning and afternoon efficiency.

When diurnal rate of change graphs of this study are folded along the noon time line, the symmetry of morning and afternoon metabolism may be compared. Some curves have larger areas before noon, some are symmetrical, and some have larger afternoon areas. In some cases assymmetry can be traced to clouds or suspected lags in exchange with plant beds. In Silver Springs the water flows down to the point of measurement about an hour after it first begins to flow across the community. In other cases explanations are not obvious. If curves like those in Figures 1, 3, and 4 were not corrected for diffusion, production would appear to be much greater in the morning than afternoon. Since it is difficult to completely eliminate artifacts due to imperfect diffusion correction, the data do not justify generalizations about small differences in morning and afternoon efficiency, although curves for clear days like those in Figure 14 may show slightly higher morning efficiency.

Summary

1. Rates of gross community photosynthesis (primary production) and total community respiration were determined with diurnal curve methods, dark bottle methods, mud bottle methods, and bell jar methods in marine waters of Texas, North Carolina, and British West Indies. Metabolic rates range from 1 to 24 gm./M^2/day oxygen. Depth of the environments range from a few centimeters of water over blue-green algal mats to 15 M of water on the Gulf of Mexico shelf.

2. Replications of the diurnal curve method at three similar stations were within 20 per cent of the mean. Two contrasting stations were within 35 per cent of the mean. Difficulties in estimating trajectory, depth, and daytime respiration are principal sources of error.

3. Diurnal curves in open shelf waters are measurable where large numbers of duplicate Winkler analyses are made.

4. Shapes and variations in diurnal curves are presented including inverted curves, curves with changing diffusion constants, curves with more morning production, curves with more afternoon production, curves indicating cloud effects and curves with midday depression.

5. Production per area is greatest in very shallow clear bays and least in turbid deeper bays where the turbidity is due to inorganic matter. Bays with bottom plants maintain relatively stable metabolism, whereas plankton-dominated bays fluctuate more widely.

6. Diurnal curve measurements generally exceed bottle measurements especially in shallow bays with benthic plant communities like Redfish Bay, Port Aransas, where diurnal curve metabolism is 100 times bottle metabolism. Bottle and free water methods may be similar in plankton blooms but ordinarily bottle methods in shallow marine waters do not provide community metabolism figures. Bottle methods were used in this study to estimate plankton activity.

7. The sum of metabolic rates from bottle measurements and bell jar measurements

was less than values from diurnal curve methods. Rate data from enclosures containing benthos are believed to be low.

8. Photosynthesis may exceed respiration on single days in all bays. but in bays with little river inflow respiration is about equal to photosynthesis within accuracy of methods. With river inflow, respiration may greatly exceed photosynthesis indicating support of the community from imported organic matter. The curve of percent saturation, indicates dominance of heterotrophic energy support when values remain undersaturated through the day.

9. In the upper Laguna Madre and Redfish Bay production is maximal in the spring-summer season and minimal in the winter season as roughly correlated with light intensities and the presence of migratory faunas.

10. Diffusion constants calculated from diurnal curve analysis range 0.5 to 3.8 gm oxygen/M^2/hr. at 0 per cent saturation. These constants are correlated with wind, current, and wave action.

11. The diffusion constant as measured with the diurnal curve method may be used to compute the steady state pollution load necessary to maintain oxygen above anaerobic levels. Total respiration (natural plus that in pollution load) must be maintained less than $R = 24\,KS + P$ (gm./M^2/day).

12. The efficiency of photosynthesis in natural community conditions is found to decrease with light intensity during the middle of the day although the total production generally increases with light intensity. A light saturation point was rarely found for community photosynthesis although in individual plants of the community. light may exceed optimum intensities for these cells.

13. Detailed instructions are given for routine bottle and diurnal curve work in shallow marine waters.

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Diurnal pH Variation in Texas Bays, and Its Application to Primary Production Estimation[1]

KILHO PARK, DONALD W. HOOD

Department of Oceanography and Meteorology
Agricultural and Mechanical College of Texas
College Station, Texas

AND

HOWARD T. ODUM

Institute of Marine Science
The University of Texas
Port Aransas, Texas

Introduction

The diurnal pH variation in marine waters is of considerable interest because it is closely related to the buffer mechanism of sea water, primary production, and some other physico-chemical processes; such as daily water temperature variation.

pH measurements in the marine environment have been relatively few. Measurement difficulties are encountered, since sea water is a relatively strong buffer solution; and the instrumentation necessary for accurate hydrogen ion concentration measurement has not been available in many cases. Sargent and Hindman (1943) have improved instrumentation with a pH meter which, they reported, had a sensitivity of approximately 0.002 pH unit. Recently, the Beckman Instruments Corporation Model G-S pH meter (sensitivity 0.0025) has been made commercially available.

In Table 1 some of the diurnal pH data from the literature are presented. For the open seas a daily change of approximately 0.05 pH unit change was reported by Moberg (1927) on the California coast near San Diego, and by Smith (1958) on the Texas Gulf Coast.

To obtain additional information on the dynamic nature of pH changes in aquatic environments, concurrent measurements of the diurnal variations in pH, phosphate (Bruce, 1959) and oxygen were made on some south Texas bays during the summer (July-August) and winter (December) of 1957.

ACKNOWLEDGMENT

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TABLE 1

Some Existing Diurnal pH Variation Data

Investigators	Min. pH	Max. pH	Δ pH	Location
*Powers (1920)	7.6	8.6	1.0	A small lagoon in Puget Sound
*Wells (1922)	.....	.....	.....	Waters over tropical banks, Tortugas, Florida
*Moberg (1927)	8.34	8.40	0.06	Mission Bay, California
	8.14	8.39	0.25	Mission Bay, California
*Nicol (1935)	8.8	9.5	0.7	Salt marsh pools in Aberlady Bay, England
	8.6	9.8	1.2	Salt marsh pools in Aberlady Bay, England
*Emery (1946)	7.5	9.0	1.5	Tide pool, near La Jolla Beach, Calif.
Odum (1956, 1957a)	7.4	7.7	0.3	Silver Springs, Florida
Schütte and Elsworth (1954)	9.1	12.6	3.5	Soft water vleis near Capetown, Africa
*Smith (1958)	8.10	8.15	0.05	Gulf of Mexico
Verduin (1956)	8.35	8.85	0.6	Western Lake Erie
	7.95	8.70	0.75	Western Lake Erie
	7.9	8.8	0.9	Western Lake Erie
McQuate (1956)	7.74	9.06	1.32	Sandusky Bay
Talling (1957)	8.3	8.7	0.4	White Nile, Africa
	8.4	8.9	0.5	Gebel Aulia, Africa
	8.3	9.0	0.7	Gebel Aulia, Africa
	8.7	9.1	0.4	Lake Victoria, Africa

* Denotes salt water environments.

THEORETICAL CONSIDERATIONS

It is apparent that solar energy is the prime cause of diurnal change in pH either directly or indirectly. Both photosynthesis and respiration of marine organisms influence the carbonic acid equilibrium system in sea water. It therefore appears feasible to calculate the magnitude of both photosynthesis and respiration by observing pH change and other supporting field data, Wells (1922) measured carbon dioxide metabolism and related it to daily pH changes at Tortugas. Harvey (1955) has summarized various aspects of the correlation between the pH and carbonic acid system in the sea, and Ryther (1956) has reviewed some of the problems with measurement of primary production by pH change.

The buffer mechanism of sea water is quite complicated. However, the most significant buffering action can be said to come from carbonic and boric acids and their salts which are present in the water. The remainder of the many weak acids in sea water may be considered to be insignificant. The magnitude of the contribution of boric acid and its salts to the buffer mechanism is approximately 5 per cent for oceanic water of a pH around 8.2 and a higher per cent for higher pH values. It is therefore necessary to consider boric acid when one computes the magnitude of primary production in the sea by diurnal pH change. A brief review of the relationship between pH and carbonic acid system in the sea follows.

From the first and second dissociation equations of carbonic acid the following relations are obtained:

$$pH = pK_1 + \log \frac{C_{HCO_3^-}}{C_{H_2CO_3}} \qquad (1)$$

$$pH = pK_2 + \log \frac{C_{CO_3^{--}}}{C_{HCO_3^-}} \qquad (2)$$

where capital C denotes molar concentration, and pK_1 and pK_2 denote the negative logarithm of the first and second dissociation constants of carbonic acid.

Assuming pK_1 and pK_2 are constant, the pH changes observed are due to changes in the ratio of bicarbonate and carbonate ions, and/or bicarbonate ion and carbonic acid. Correction for boric acid contribution on pH changes must be made. Therefore, any change of the relative concentration of carbonic acid components, H_2CO_3, HCO_3^-, and CO_3^{--}, due to photosynthesis and respiration of aquatic organisms, tends to change the pH of the water.

The dissociation constants of both carbonic and boric acids in sea water are given by Buch (1951) and Lyman (1957) as functions of temperature and chlorinity. Lyman's constants are used in this paper. His apparent first and second dissociation constants for carbonic acid are defined as:

$$K_1' = \frac{A_{H^+} C_{HCO_3^-}}{A_{(H_2CO_3 + CO_2)}} \qquad (3)$$

$$K_2' = \frac{A_{H^+} C_{CO_3^{--}}}{C_{HCO_3^-}} \qquad (4)$$

where A denotes active concentration.

Solar energy also changes the temperature of the water thus affecting pH. Buch and Nynäs (1939) studied the relationship between temperature and pH in a closed system. They found that pH falls with rising temperature at a magnitude dependent upon the pH and salinity of the water. At a chlorinity of 19.5‰, a temperature range of 20–30° C, and a pH of 8.2, the pH falls 0.01 unit per each 1° C rise in temperature.

If one could assume environmental changes are restricted to temperature changes, one would expect the minimum pH to occur at the time of highest water temperature. Hence the minimum pH would be during daylight hours when the water temperature is maximum, and maximum during night when the water temperature is lowest. This trend is opposite to the pH changes which one would expect from biological activity.

If diffusion due to changes in solubility of molecular CO_2 is unimportant, a pH change caused by temperature change does not affect the total carbon dioxide content of the water. In computations of the concentration of carbon dioxide components in the environment, temperature errors are minor since the constants used are corrected for temperature.

In an environment in which calcium carbonate precipitation and dissolution are active, pH change due to biological CO_2 removal may be obscured unless a precise knowledge of the quantity of precipitate is obtainable since calcium carbonate affects buffering action. Another complication is the diffusion exchange of carbon dioxide across the air-water interface. The diffusional problem needs much more detailed investigation.

Stations

Four stations were selected for this study. The productivity of these stations was studied by Odum and Hoskin (1958) by means of the diurnal oxygen method. The locations of the stations are given in Figure 1. All stations were representative of large areas of the shallow bays, ranging from 1 foot to 6 feet in depth.

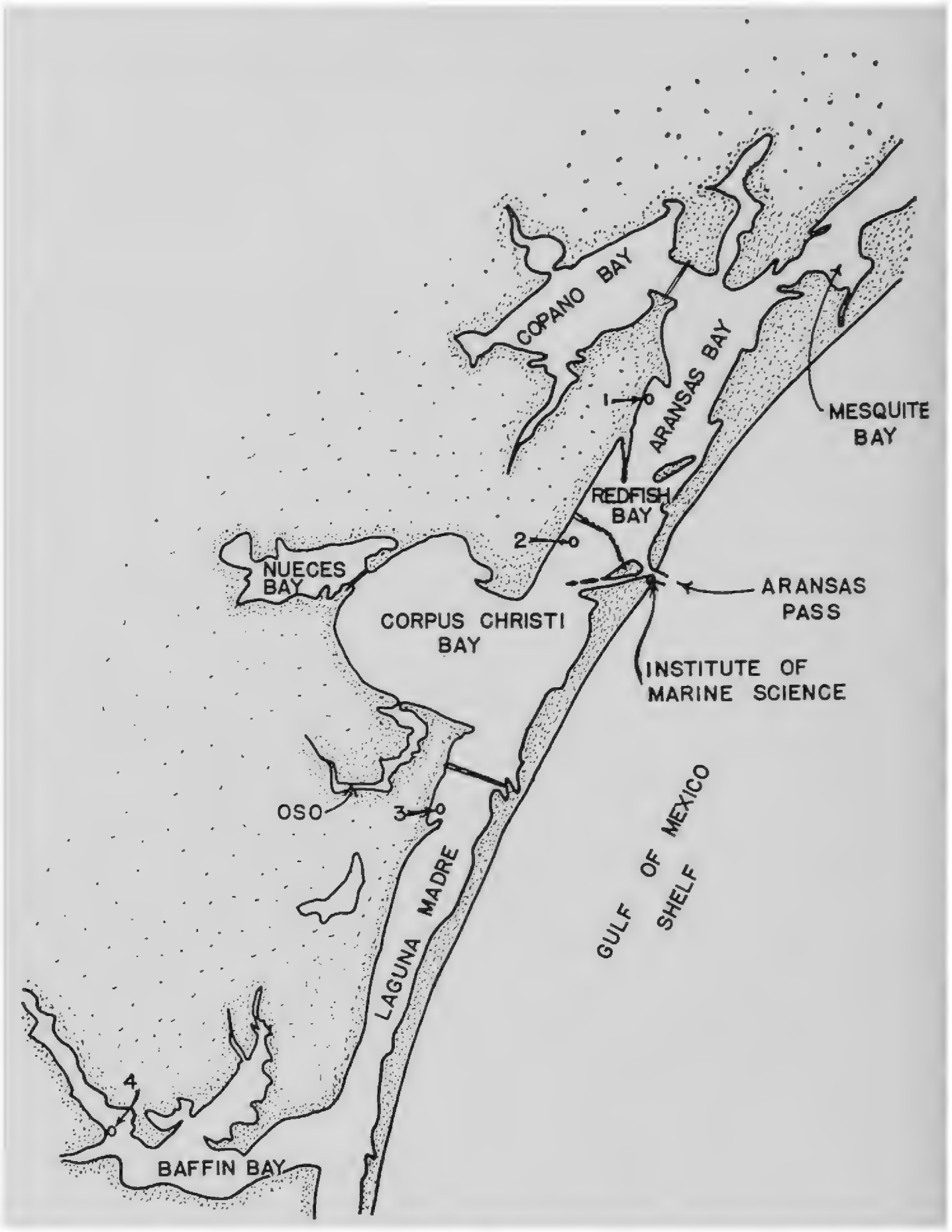


FIG. 1. Locations of stations occupied in diurnal pH measurements in Texas bays: Rockport Basin, 1; Redfish Bay station, 2; Laguna Madre station, 3; Baffin Bay station, 4.

Redfish Bay was the shallowest of the bays studied (approximately 1 foot deep) and had the heaviest growth of benthic "grasses" (*Thalassia* and *Ruppia*). The "grasses" emerged at low tide. The water mass at the station was thought to be relatively stationary.

The Laguna Madre station was midway between Pita Island and the Texas mainland in about 2 feet of water. A fairly heavy growth of *Diplanthera* "grass" existed.

The Baffin Bay area was about 5 feet in depth. The water was turbid with a visibility of not over 2 feet. The chlorinity of the water exceeded 30‰.

The Rockport station was in the Rockport Yacht Basin in water about 6 feet deep. During the investigation the water surfaces became intermittently covered with oil slicks.

Methods

Measurements of pH were made with a Beckman Model G-S pH meter. The meter was enclosed, with desiccant, in a transparent polyethylene bag to exclude salt air. Both the glass and calomel electrodes were the general purpose extension type used with all laboratory models of Beckman Instruments. The electrodes were inserted through a No. 11 rubber stopper fitted to a glass container in which the pH of water samples was measured. Standard buffer solution of pH 7.00 was kept at the water temperature by partially immersing the container in the sea water, thus eliminating the temperature correction between the water and buffer solution.

Water samples were either taken by filling the bottles at the appropriate depth by hand or measurements were taken by inserting the electrodes directly into the water. In the former case the pH was measured as quickly as possible and without exposure to air. Although the Beckman Model G-S pH meter has been found sensitive to 0.003 pH units, with the possibility of greater field errors, the pH value was recorded to 0.01 unit.

In order to obtain carbonate alkalinity of the water samples both titration alkalinity and total inorganic boron analyses were made on samples collected at three-hour intervals. Boron samples were frozen in dry ice until the analyses were made. The titration alkalinity was determined according to the method of Wattenberg (1933) using a pH of 6.0 at the end point. The total inorganic boron was measured by the method of Noakes (1959).

Results and Discussion

The field data obtained at the four stations are presented in Figures 2 through 5 and summarized in Table 2.

Table 2

Observed Field Data During the Investigation of Diurnal pH Variation in Texas Coastal Waters

Location	Date (1957)	pH Range	△pH	Temp. Range (° C.)	Cl‰	Titration Alkalinity (Milliequivalent/l) Range	Average	Total Inorganic Boron (Millimol/l)
Baffin Bay	July 26–27	8.20–8.34	0.14	29.0–32.0	31.8	4.01–4.13	4.09	0.90
	Aug. 15–16	7.94–8.35	0.41	29.0–32.0	36.1	4.34–4.39	4.37	1.10
	Dec. 22–23	8.52–8.62	0.10	19.2–21.2	34.9	3.69–3.80	3.74	0.87
Redfish Bay	July 18–19	8.23–8.91	0.68	28.0–35.0	16.6	2.45–2.65	2.53	0.37
	Dec. 25–26	7.98–8.41	0.43	18.0–23.0	15.7	2.92–3.01	2.95	0.61
Laguna Madre	Aug. 1–2	8.15–8.42	0.27	27.4–32.0	31.6	2.83–2.95	2.86	0.92
	Dec. 28–29	8.21–8.49	0.28	14.4–17.5	17.6	2.82–2.88	2.85	0.40
Rockport	Aug. 5–6	8.37–8.44	0.07	31.0–32.0	18.9	2.82–3.02	2.88	0.64

From the analyses it was observed that titration alkalinity and inorganic boron did not show a regular diurnal cycle but were about the same throughout the 24-hour period. Chlorinity differed quite markedly from station to station ranging from approximately 16‰ at Redfish Bay to 36‰ at Baffin Bay.

In comparison with other stations Redfish Bay showed the largest diurnal variation in

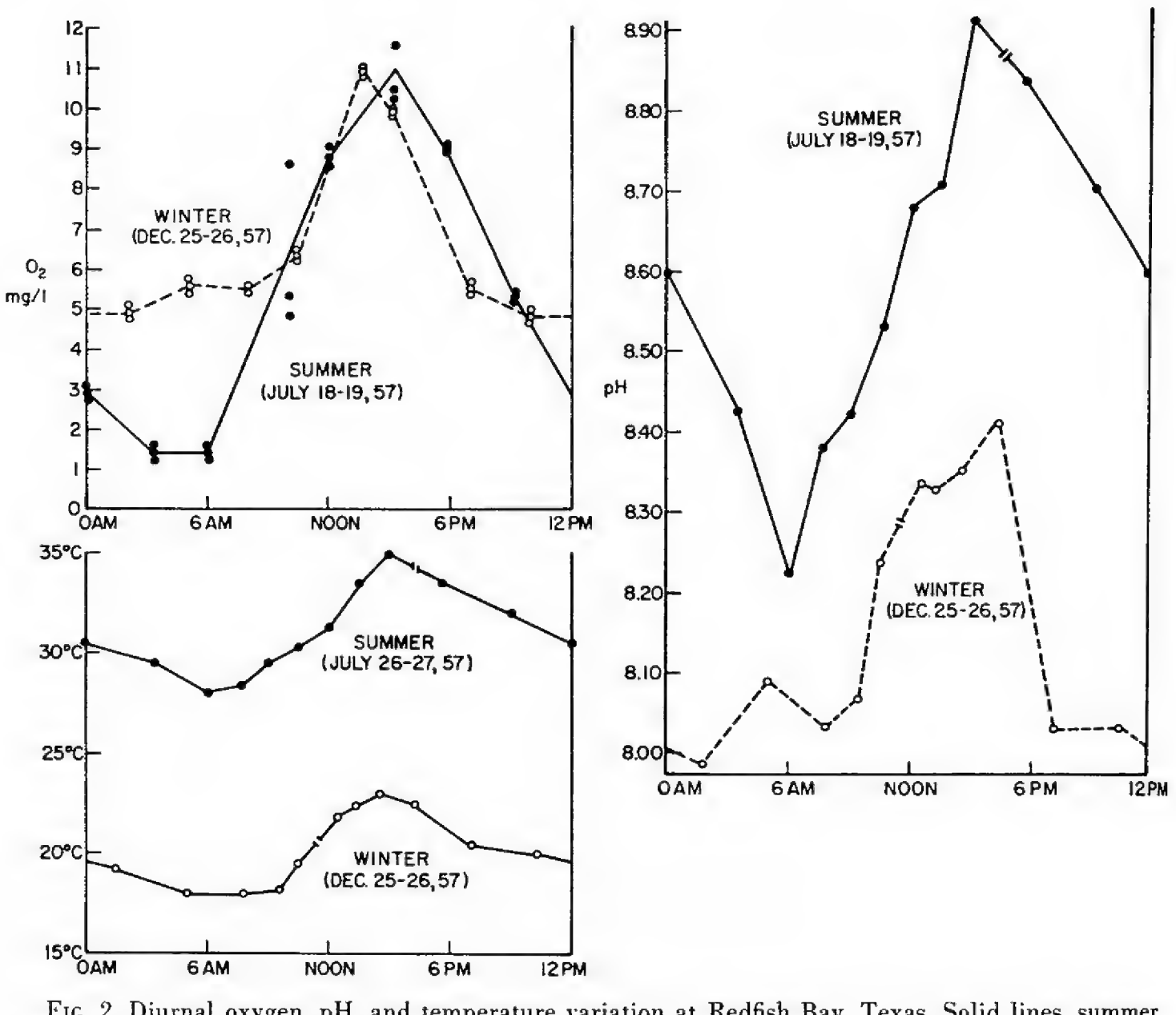


FIG. 2. Diurnal oxygen, pH, and temperature variation at Redfish Bay, Texas. Solid lines, summer data for July 18–19, 1957. Dotted lines, winter data for Dec. 25–26, 1957.

dissolved oxygen, temperature and pH (Fig. 2). The values of pH and temperature from this station in summer were higher and showed a greater diurnal range than in the winter. However, in the Laguna Madre a higher pH was observed in the winter than in the summer.

Three sets of diurnal pH values were obtained in Baffin Bay (Fig. 4). Winter pH values were higher than the summer, but diurnal changes were less. The two summer stations showed a marked difference in the magnitude of diurnal pH change although the variation of oxygen and temperature were almost the same.

The Rockport station (Fig. 5) was occupied after a dinoflagellate bloom. This station had the least diurnal variation in dissolved oxygen, pH and temperature of the locations studied. A maximum was observed at 1800 hrs. which was quite different from that at other stations. The amplitude of diurnal oxygen and pH was less in the deeper environments where the effects of metabolism were dispersed in a greater volume of water.

DIURNAL VARIATION OF TOTAL CARBON DIOXIDE

Using the data for pH and carbonate alkalinity, the total carbon dioxide components, $C_{CO_3^{--}}$, $C_{HCO_3^-}$, $C_{H_2CO_3}$ and C_{CO_2} can be calculated at any given time of the day. The equations for this computation are summarized as follows:

$$C_{HCO_3^-} = \text{Carbonate Alkalinity} \frac{A_{H^+}}{2K'_2 + A_{H^+}} \text{ gm.-ion/L} \qquad (5)$$

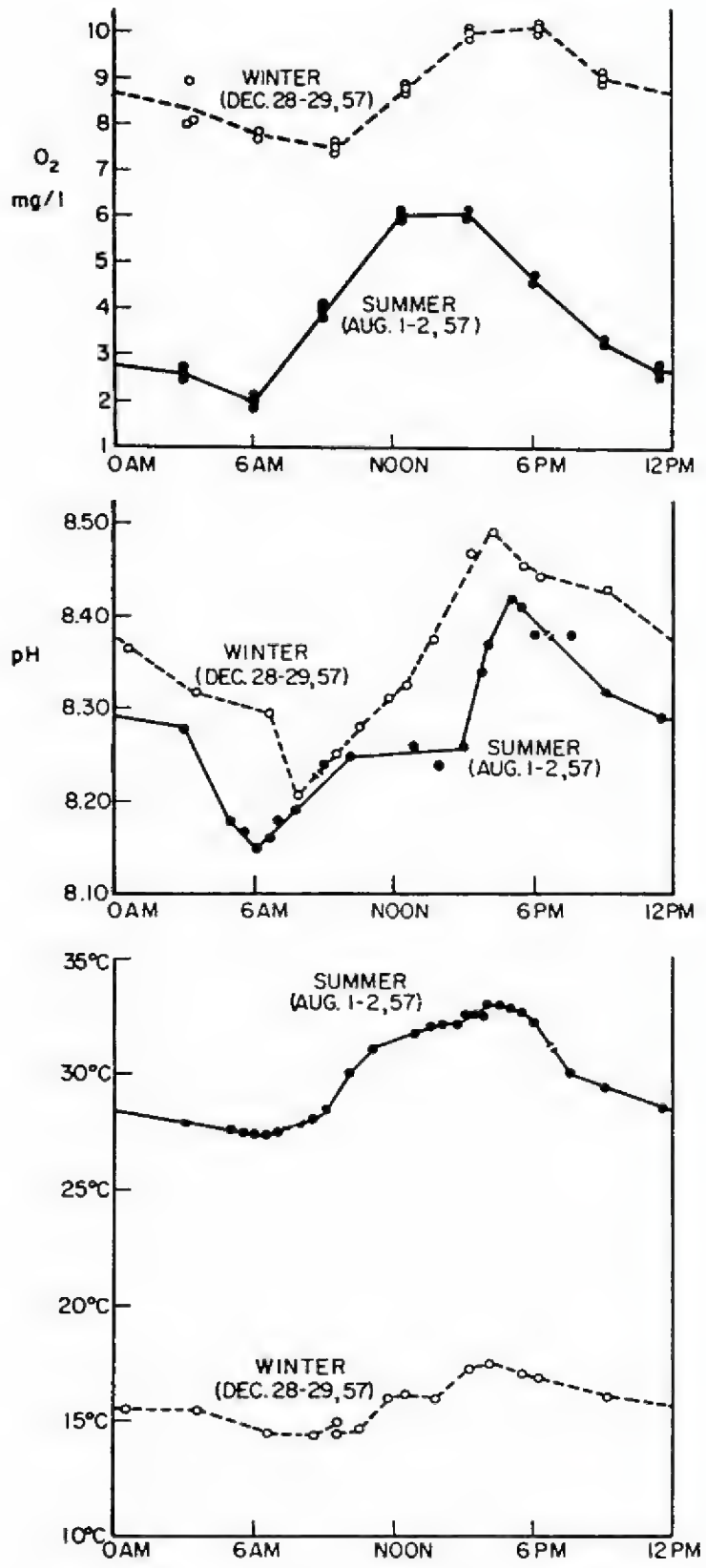


FIG. 3. Diurnal oxygen, pH, and temperature variation near Pita Island, Laguna Madre, Texas. Solid lines, summer data for Aug. 1–2, 1957. Dotted lines, winter data for Dec. 28–29, 1957.

$$C_{CO_3^{--}} = \text{Carbonate Alkalinity} \frac{K'_2}{2K'_2 + A_{H^-}} \text{ gm.-ion/L} \qquad (6)$$

$$C_{(CO_2 + H_2CO_3)} = \frac{A_{H^-} C_{HCO_3^-}}{K'_1} \text{ gm.-Mole/L} \qquad (7)$$

Let the total components of the carbon-dioxide system be represented by $\sum CO_2$:

$$\sum CO_2 = C_{CO_3^{--}} + C_{HCO_3^-} + C_{(CO_2 + H_2CO_3)}$$

Then:

$$\sum CO_2 = \text{Carbonate Alkalinity} \frac{A_{H^+} + K'_2 \left(1 + \frac{A_{H^+}}{K'_1}\right)}{2K'_2 + A_{H^-}} \text{ gm.-Mole L} \qquad (8)$$

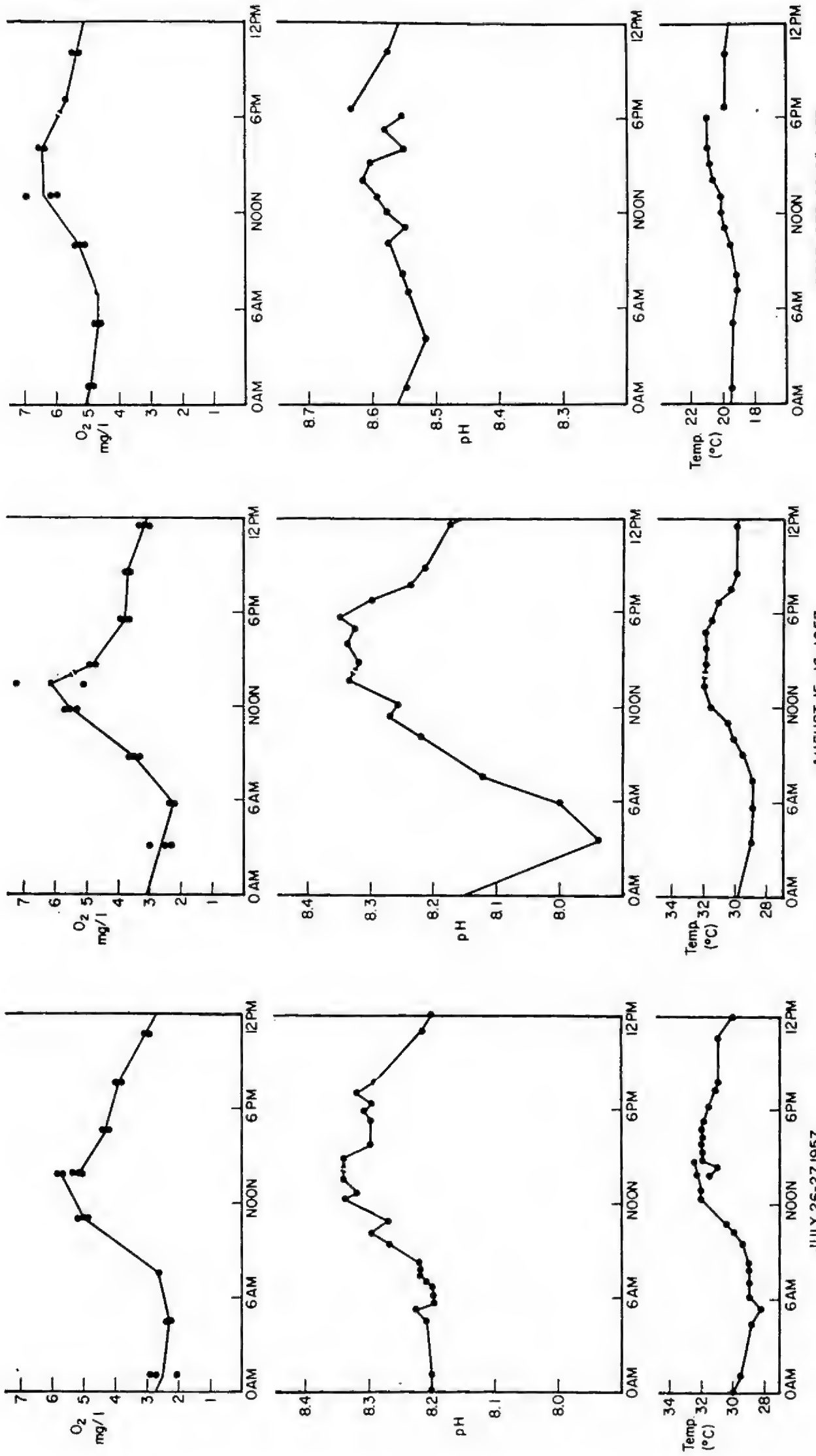
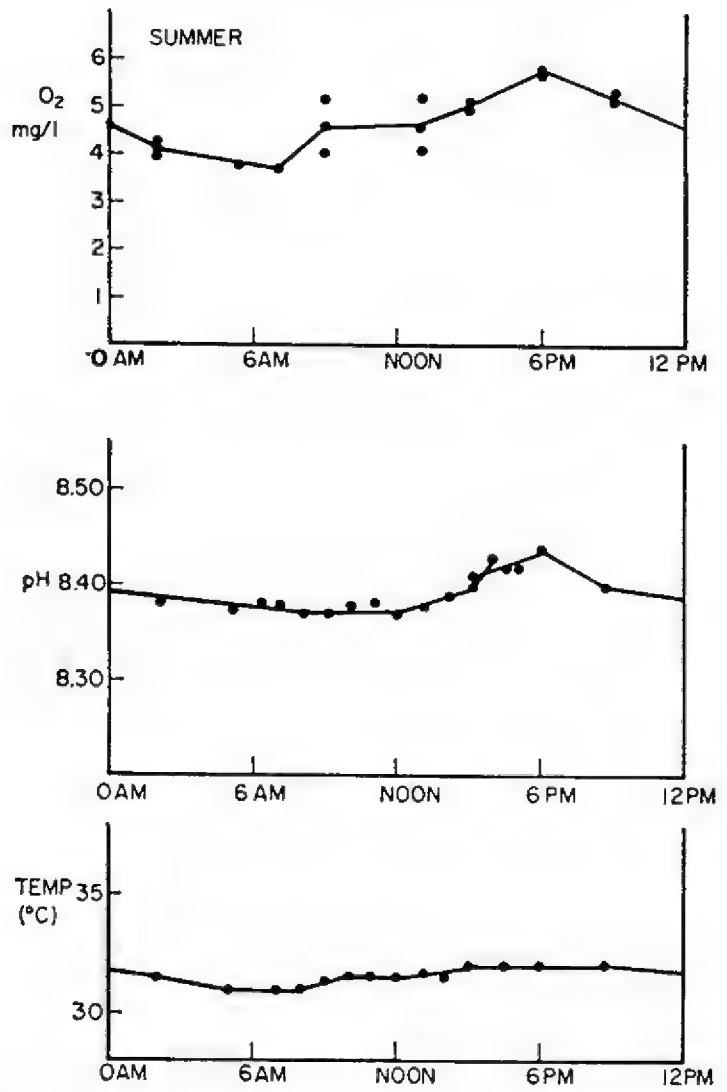


FIG. 4. Diurnal oxygen, pH, and temperature variation at Baffin Bay, Texas, July 26–27, Aug. 15–16, Dec. 22–23, 1957.

From equation 8 the average total CO_2 components were plotted by hour in Figures 6 to 13. For purposes of comparison diurnal oxygen results were also plotted. The rate of change of total CO_2 was plotted as was the per cent saturation of molecular CO_2 calculated from Buch's data (Buch, 1951).



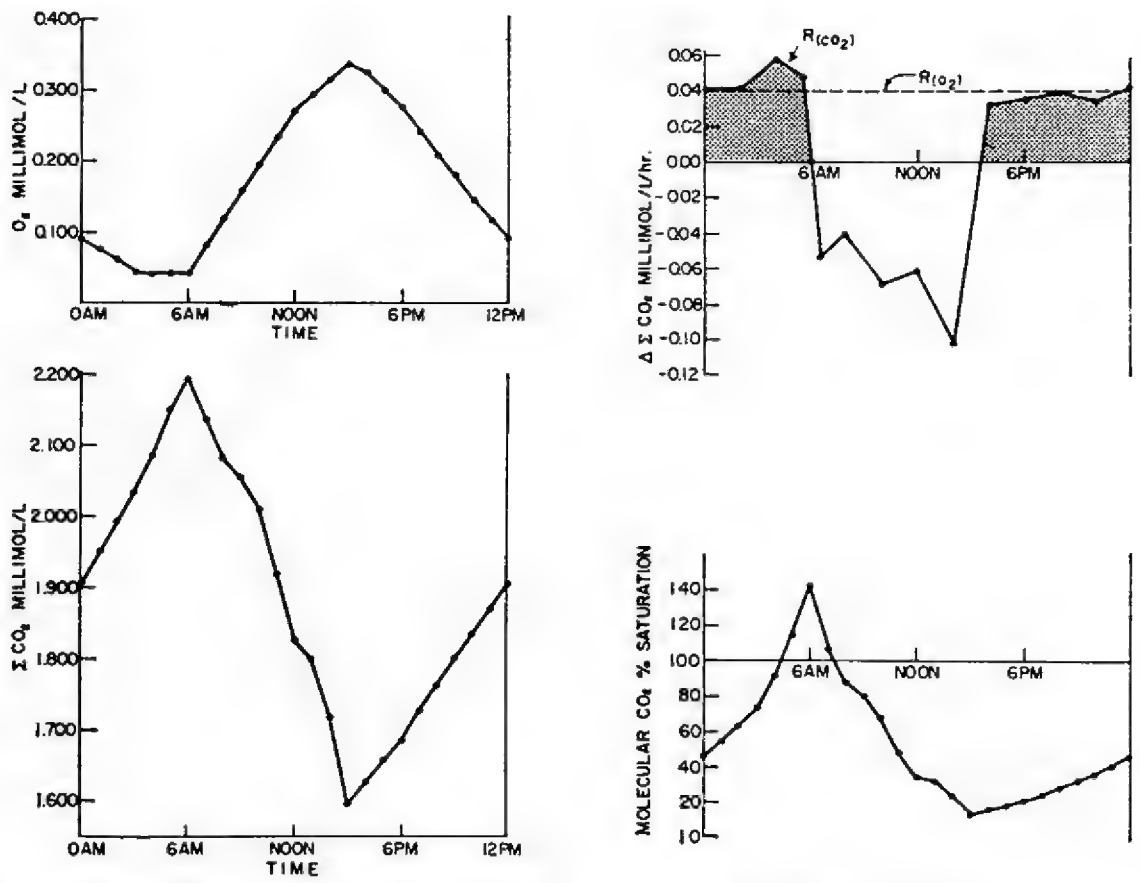


FIG. 6. Diurnal computations for Redfish Bay, July 18–19, 1957. Hourly variation of dissolved oxygen, total carbon dioxide components $[C_{CO_3^{--}} + C_{HCO_3^-} + C_{(CO_2 + H_2CO_3)}]$, rate of change of total carbon-dioxide, and per cent saturation of molecular carbon-dioxide. The dotted line, $R_{(O_2)}$, is the nighttime rate of respiration computed from the diurnal oxygen method (Odum, 1956). The nighttime rate of respiration was also computed from carbon dioxide by estimating the shaded area between the night rate of change, $R_{(CO_2)}$, and zero.

Estimation of Primary Production

Assuming the diurnal variation of total CO_2 was largely due to photosynthesis and respiration, the estimation of primary production can be performed by the diurnal curve method (Odum, 1956).

From oxygen studies with diurnal curves, Odum and Hoskin (1958) found the oxygen diffusion constant for these Texas bays to be about 1 gm. $O_2/M^2/hr.$ for 0.2 atmosphere saturation gradient between atmosphere and water. A diffusion coefficient of similar order of magnitude for carbon dioxide may be expected for the same conditions of wave motion and turbulence. With no free carbon dioxide at all in the water the rate of diffusion of the carbon dioxide from the air would be about 6.7 gm. $CO_2/M^2/$ gradient of one atmosphere. Since the partial pressure of CO_2 in the air is only about 3×10^{-4} atmospheres, the maximum diffusion rate expected into the water during the middle of the day is about 1.5 mg./M^2/hr. and negligible compared to the respiration rates, which are 100 to 1000 times as great in these bays.

It is of considerable interest, that observations of the carbon dioxide content of the sea and air during the International Geophysical Year show that equilibrium seldom exists. In some 10,000 miles of oceanic observations in the Gulf of Mexico, Caribbean and Middle Atlantic (Ibert and Hood, 1958), only rarely was it observed that the carbon dioxide concentration of air and the sea were the same. In most cases the concentration in the air was high with respect to that of the sea. Diffusion of carbon dioxide into the sea surface is evidently slow or the conditions evidenced could not persist.

In the summer in Redfish Bay there was a change in total CO_2 content of the water of 0.6 mM/L during the period from 0600 to 1500 Central Standard Time. From sunrise to late afternoon the rate of decrease of total CO_2 was nearly constant. The rate of increase of CO_2 due to the summation of respiration and diffusion was also nearly constant throughout the dark hours.

With the low partial pressure of CO_2 gas in both air and water, diffusion was negligible. Thus the graph of night rate of change is apparently a record of the course of community respiration. In order to obtain a value for respiration, the graphical areas between the rate of change curves for CO_2 during the dark hours and the zero lines were estimated (Figs. 6–13, shaded areas). The average respiration rates found at night were used to estimate the daytime respiration. For comparison, the dotted line R is plotted in these figures to indicate the respiration correction as computed from the oxygen method (Odum and Hoskin. 1958). At the summer station in Redfish Bay (Fig. 6) the value for respiration obtained from oxygen data and that from carbon dioxide are nearly the same. The respiratory quotient for this station was, thus, found to be 1. The gross primary production was then obtained by estimation of the area of the rate curve beneath the respiration value. The gross primary production, P_G, was found to be 0.92mM/L/day. Data from the other stations were handled in the same manner and the estimated gross primary production rates are given in Table 3.

Hourly changes in the CO_2 system components (CO_2, HCO_3^-, CO_3^{--} and H_2CO_3) based on the diurnal pH variation data for the summer station at Redfish Bay are shown in Figure 14. The bicarbonate ion changes most, followed by carbonate ion and carbonic acid. Dissolved carbon dixoide (and carbonic acid) represent only a small portion, less than 1 per cent of total CO_2 content in the water. Observations of Hood, Park,

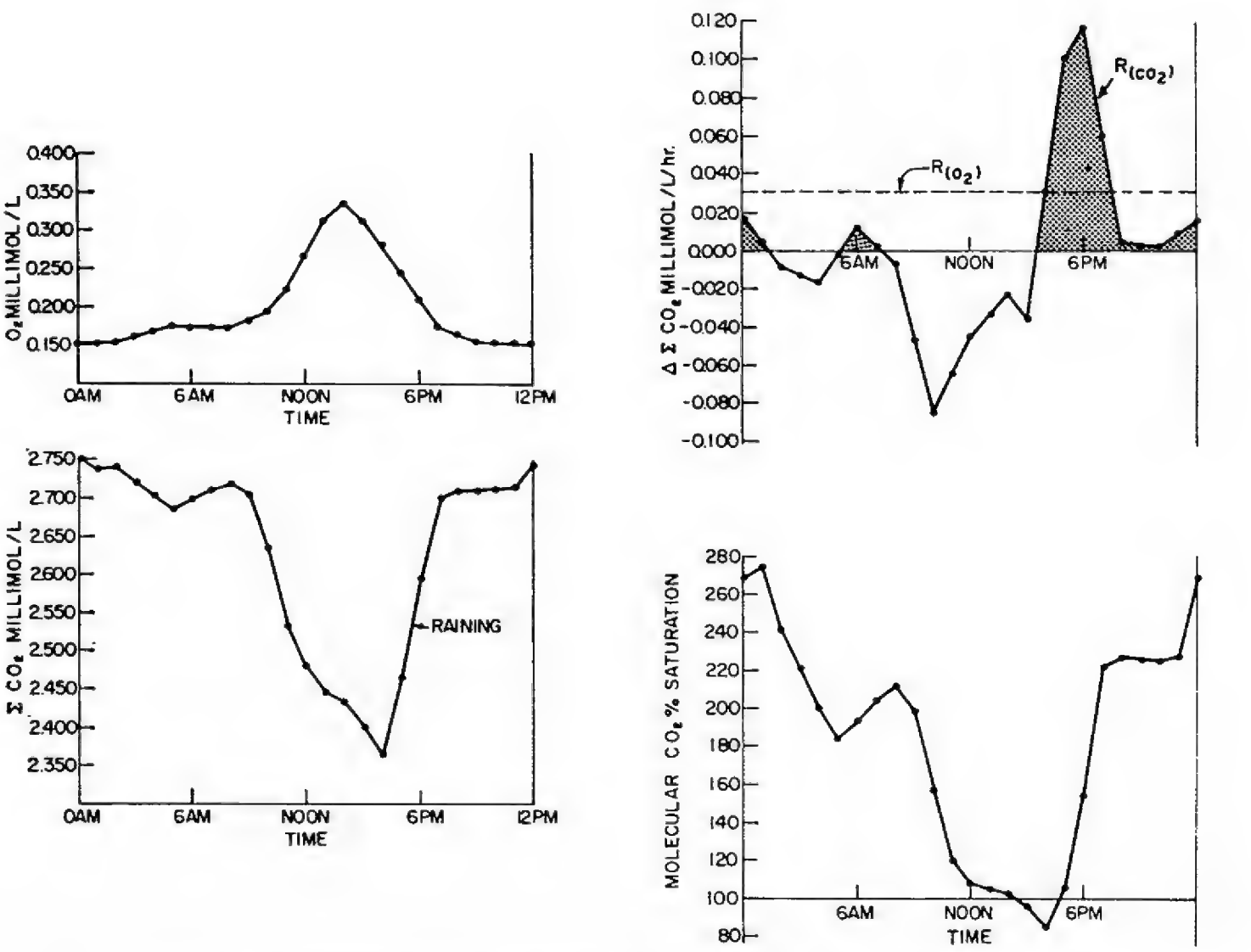


FIG. 7. Diurnal computations for Redfish Bay, Dec. 25–26, 1957. See legend for Figure 6.

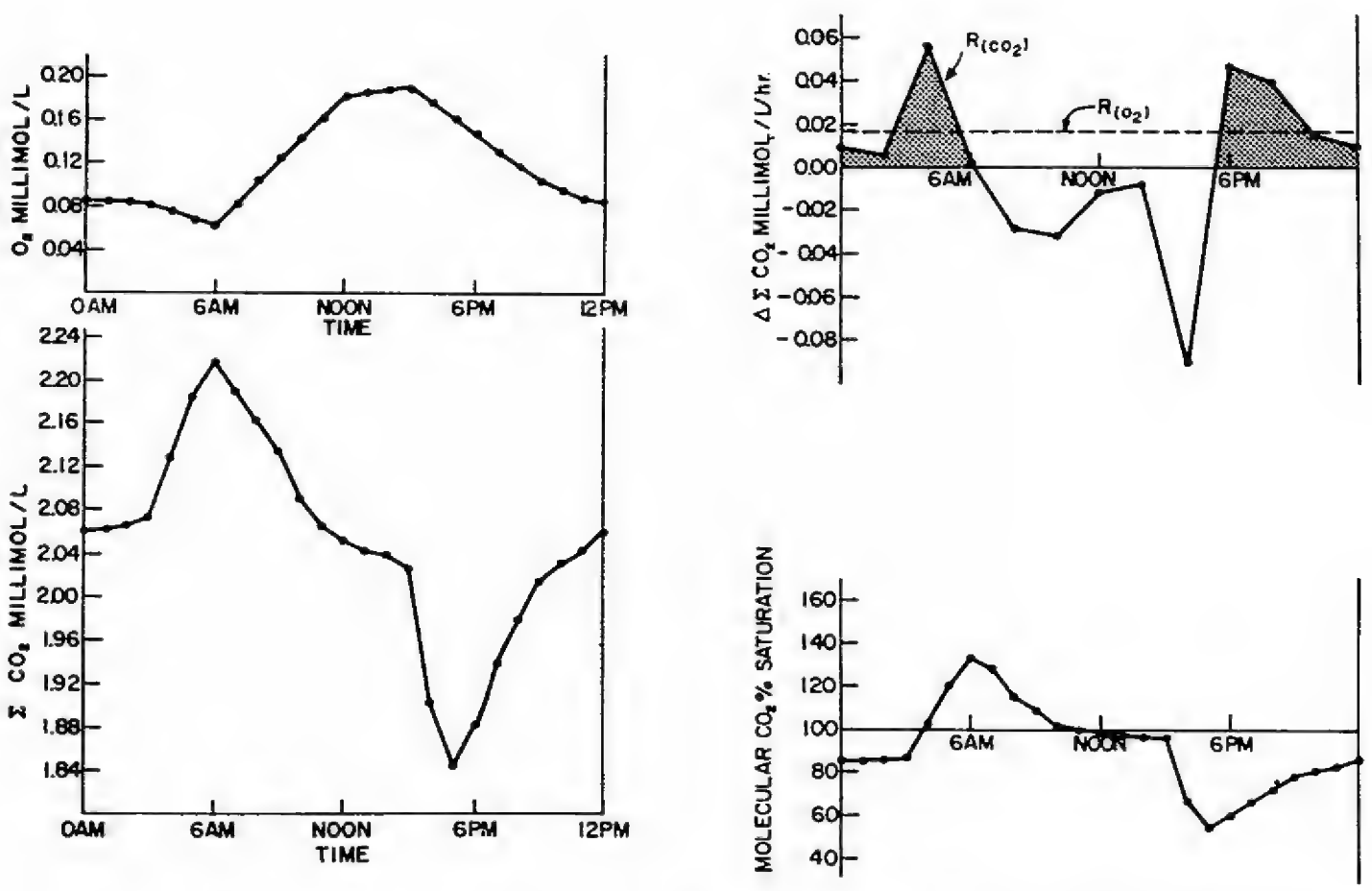


FIG. 8. Diurnal computations for Laguna Madre, Aug. 1–2, 1957. See legend for Figure 6.

TABLE 3

Comparison of Gross Primary Production and Respiration Estimations by O_2 and pH Measurements in Highly Productive Texas Coastal Bays

		Gross Primary Production			Respiration Estimation		
Location	(Date (1957)	O_2 Method mM/L/day	CO_2 Method mM/L/day	PQ O_2/CO_2	O_2 Method mM/L/day	CO_2 Method mM/L/day	RQ O_2/CO_2
Baffin Bay	July 26–27	0.27	0.31	0.9	0.48	0.31	1.5
	Aug. 15–16	0.24	0.90	0.3	0.30	0.91	0.3
	Dec. 22–23	0.16	0.19	0.8	0.23	0.29	0.8
Redfish Bay	July 18–19	0.88	0.92	1.0	0.96	1.00	1.0
	Dec. 25–26	0.43	0.68	0.6	0.75	0.49	1.5
Laguna Madre	Aug. 1–2	0.25	0.56	0.4	0.41	0.58	0.7
	Dec. 28–29	0.17	0.27	0.6	0.15	0.25	0.6
Rockport Basin	Aug. 5–6	0.13	0.12	1.0	0.24	0.12	2.0

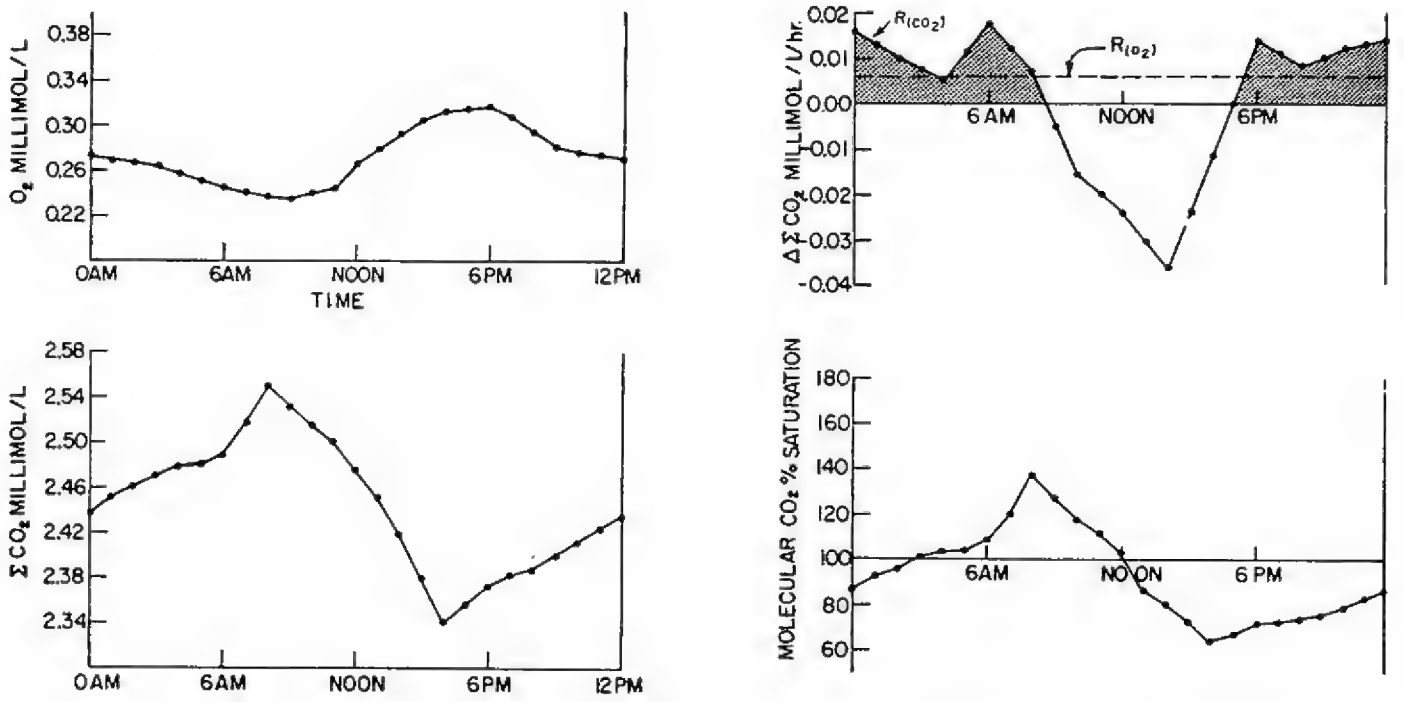


FIG. 9. Diurnal computations for Laguna Madre, Dec. 28–29, 1957. See legend for Figure 6.

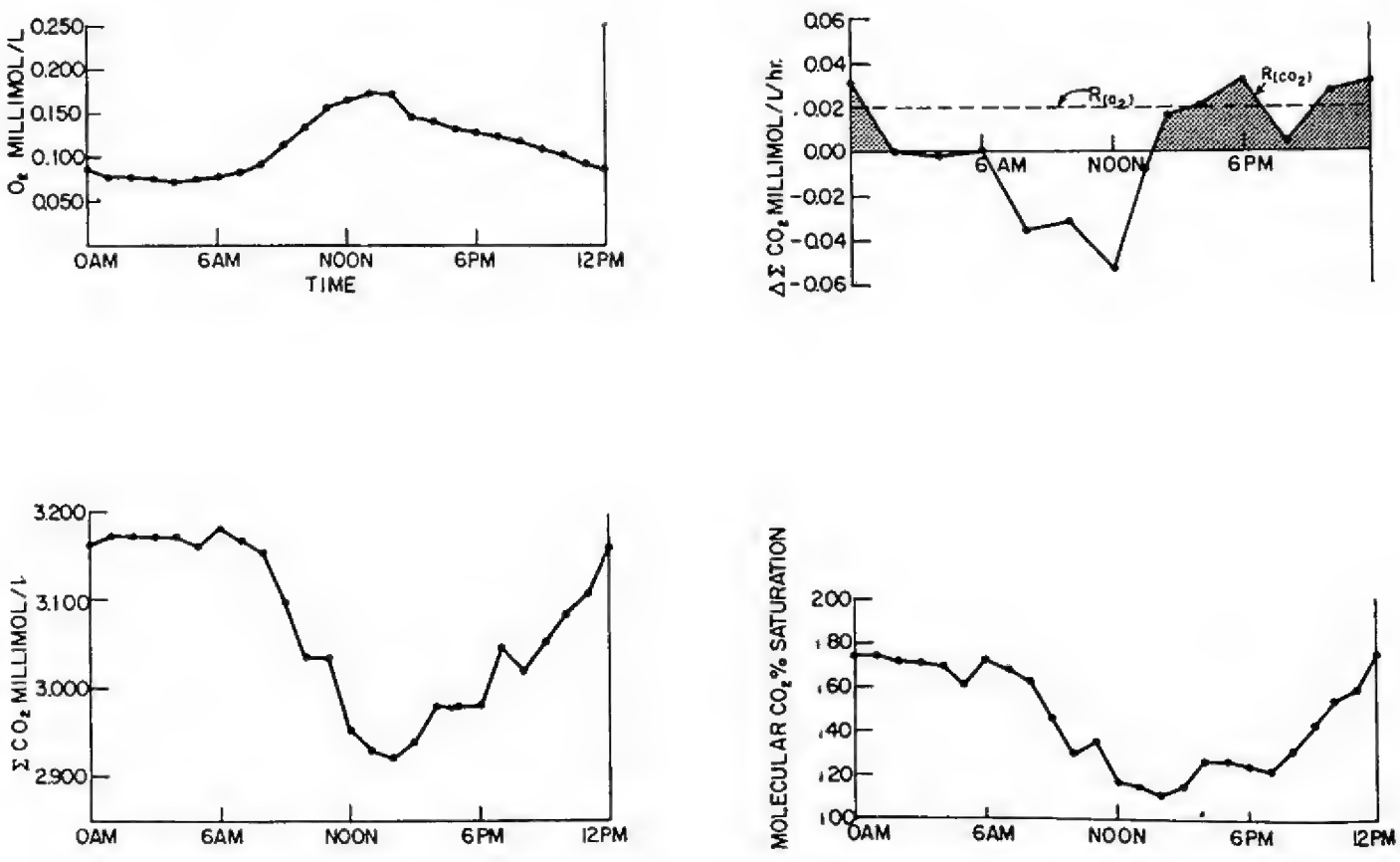


FIG. 10. Diurnal computations for Baffin Bay, July 26–27, 1957. See legend for Figure 6.

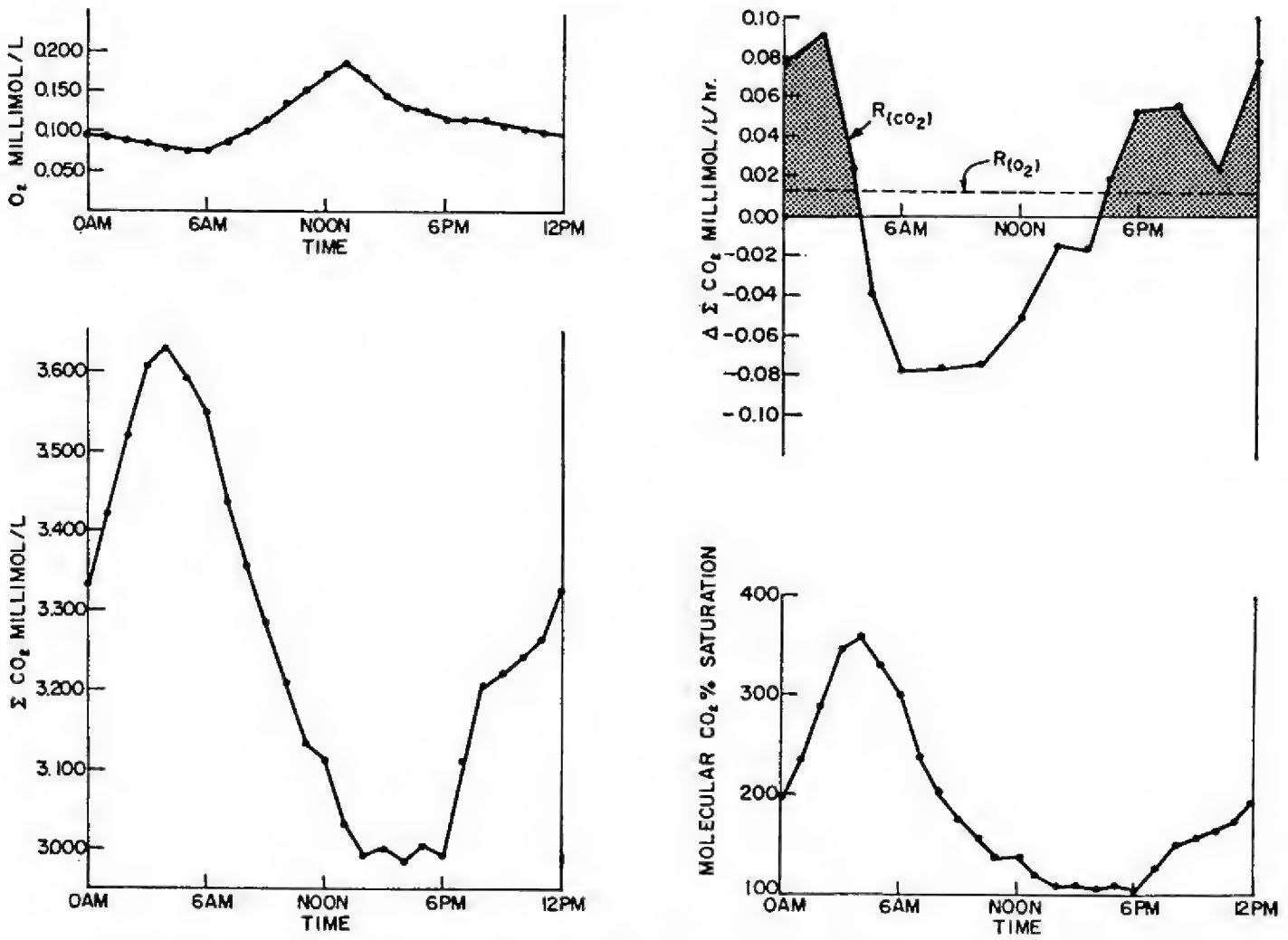


FIG. 11. Diurnal computations for Baffin Bay, Aug. 15–16, 1957. See legend for Figure 6.

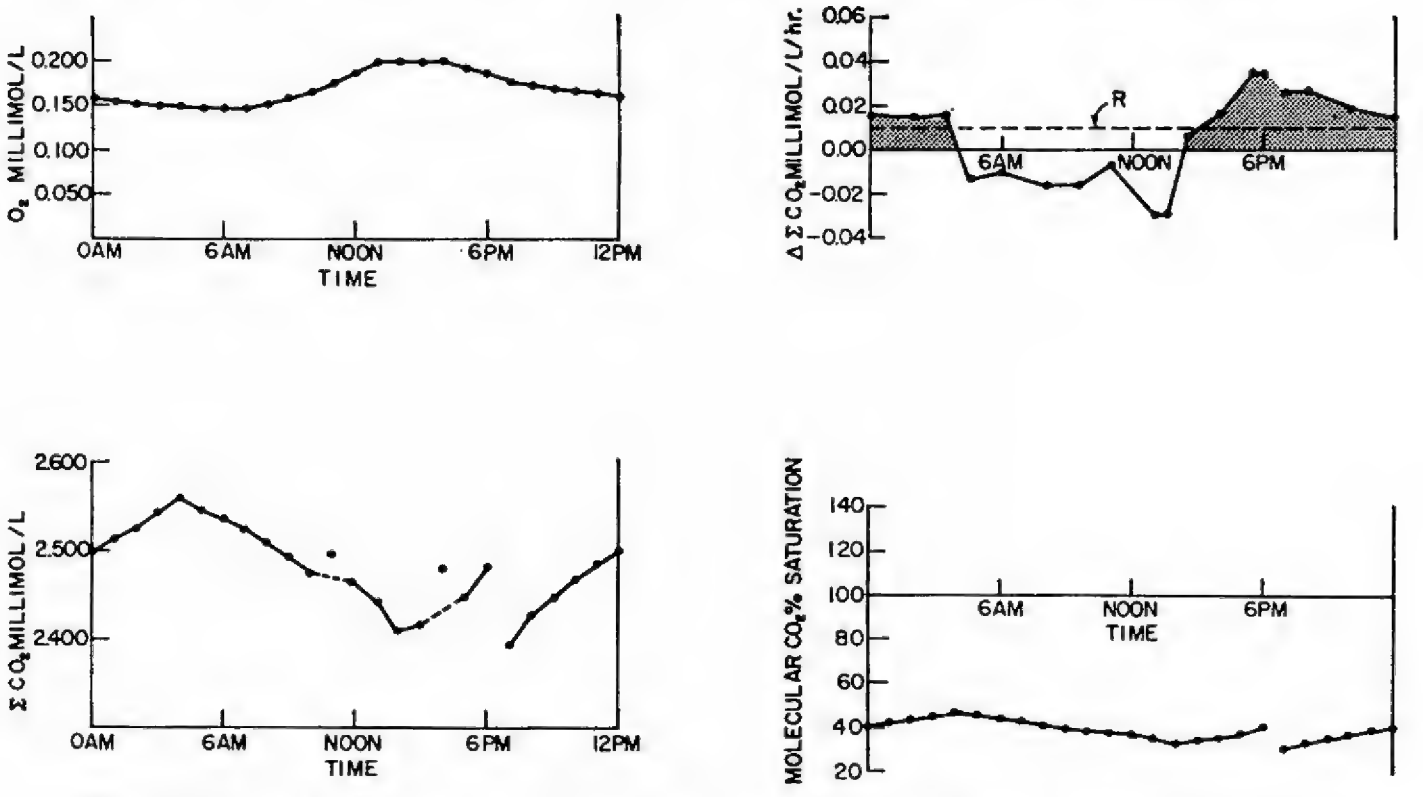


FIG. 12. Diurnal computations for Baffin Bay, Dec. 22–23, 1957. See legend for Figure 6.

and Smith (1958) show that many marine plants tend to utilize bicarbonate ion directly as a source of carbon in photosynthesis.

EFFECT OF COLD FRONT AND HEAVY SHOWERS ON TOTAL CARBON DIOXIDE CONTENT

At the winter station on Redfish Bay (Figs. 2 and 7) relatively heavy rainfall fell accompanied by a cold front between 1600 and 1900 Central Standard Time December 25, 1957. During a period of 3 hours the pH of the water dropped abruptly from

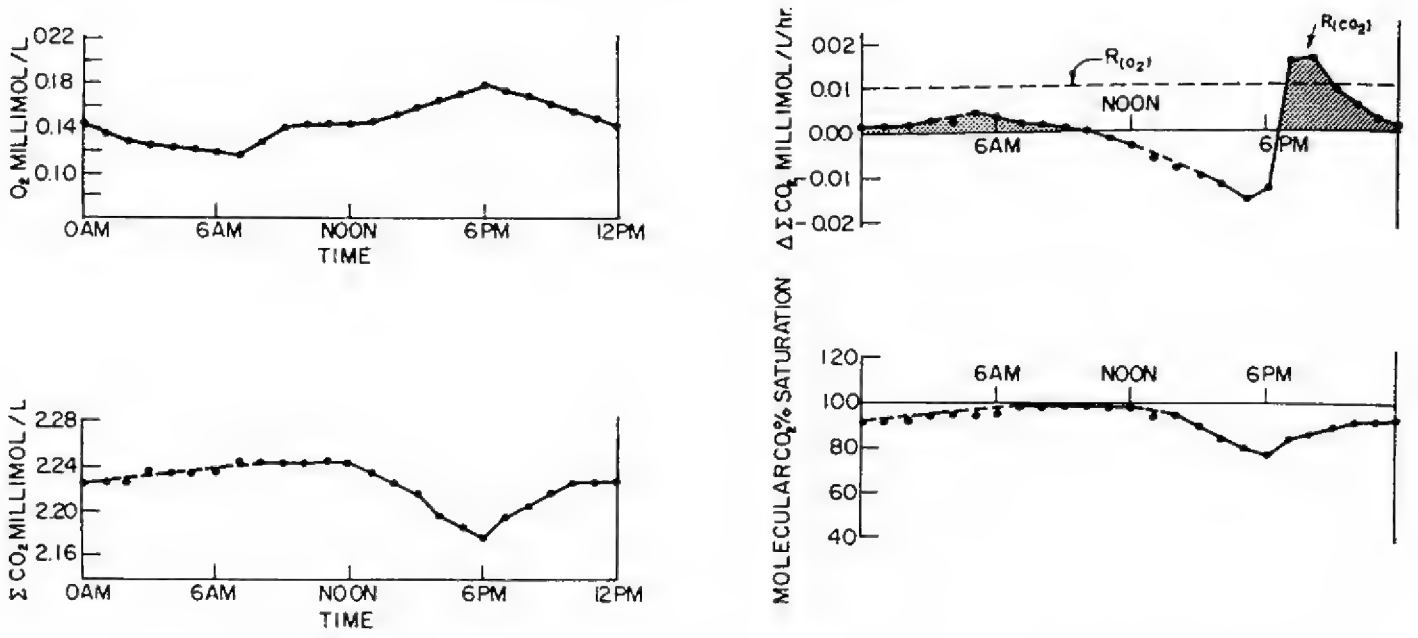


FIG. 13. Diurnal computations for Rockport Basin, Aug. 5–6, 1957. See legend for Figure 6.

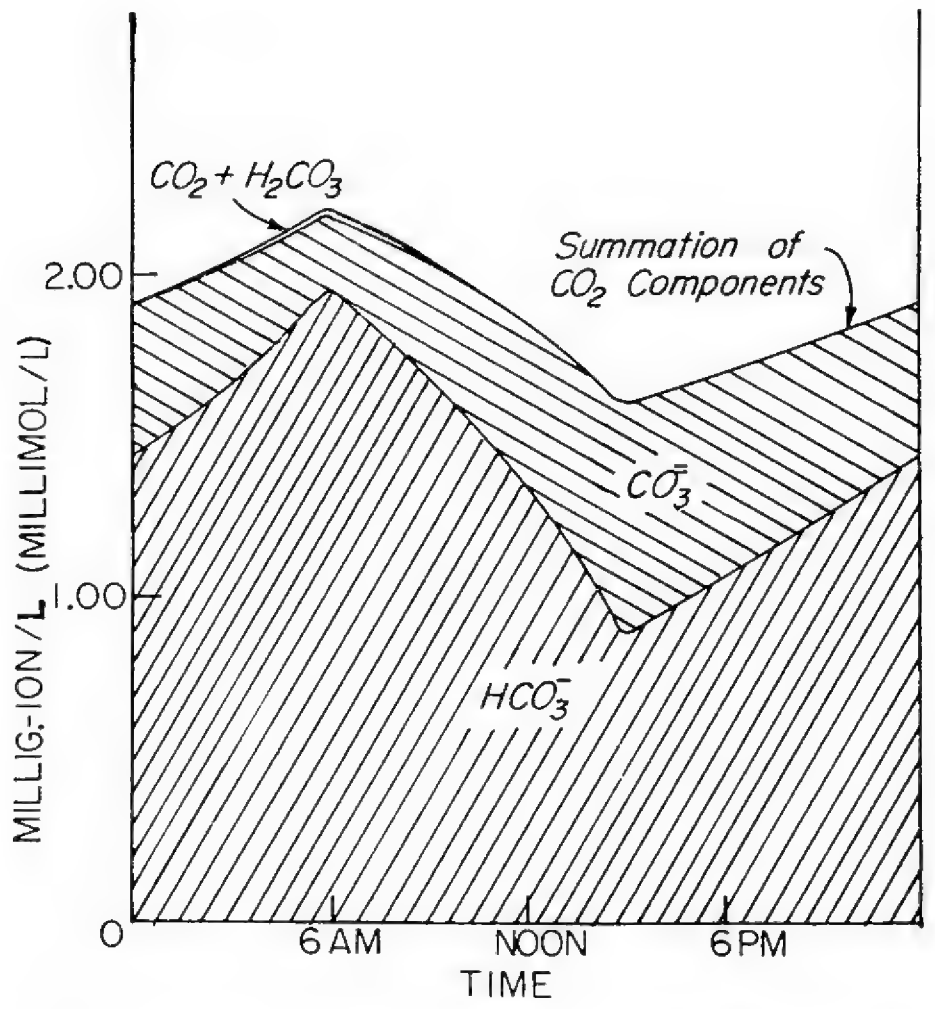


FIG. 14. Change in the components of the carbon-dioxide system based on data from Redfish Bay, Texas, July 18–19, 1957.

8.41 to 8.03 and the temperature from 22.4° C to 20.4° C. These changes are more rapid than those normally observed due to a decrease in light intensity and appear to be caused by increased diffusion rates and/or by addition of CO_2 rich fresh water through rainfall. The rain storm greatly increased surface agitation and mixing rates, resulting in increased carbon dioxide invasion of the bay waters.

The over-all effect of the rain storm may be estimated from the data shown in Figure 15. The total CO_2 content of the water was increased by approximately 0.33 mM/L in 3 hours during rainfall. The photosynthesis during this period was minimal because of

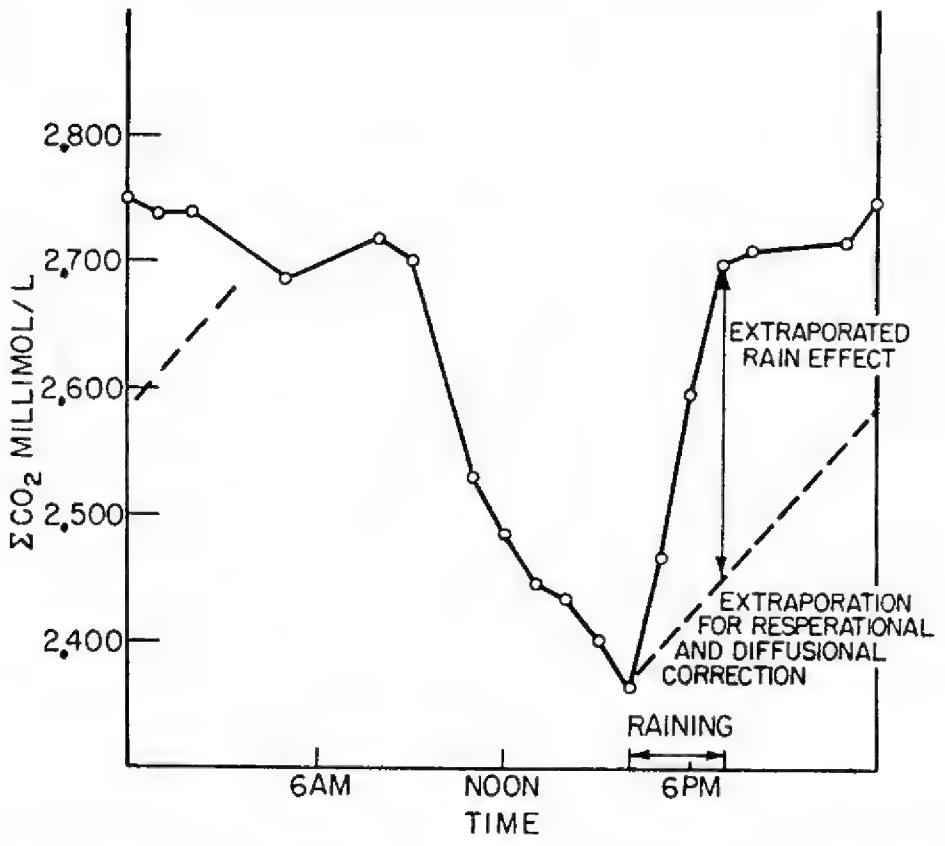


FIG. 15. Estimation of the effect of rain by extrapolation of data from Figure 7.

the low light intensity. Assuming the respiration had the similar tendency to that shown in Figures 6 and 9, it seems reasonable to draw a relatively straight line from 1600, the start of the rain, to 0600 next morning. From the extrapolation a correction value of approximately 0.08 mM CO_2 was obtained. The net change of CO_2 due to the storm was 0.25 mM/L/3 hours or 0.08 mM/L/hr. It is interesting that similar changes have been observed with respect to dissolved molecular carbon dioxide in the Caribbean during the summer of 1958 (Ibert and Hood, 1958).

PHOTOSYNTHETIC AND RESPIRATORY QUOTIENTS

Both photosynthetic ($PQ = O_2/CO_2$ by molecules and respiratory quotients ($RQ = O_2/CO_2$ by molecules), based on the field data obtained, cover a wide range of values. PQ, from 0.3 to 1.0, and RQ, of 0.3 to 2.0, were observed (Table 3).

Ryther (1956) reviewed and summarized the existing measurements of PQ in plankton reporting values which are rather close to unity, as expected for the synthesis of carbohydrates. Calculations of PQ can be made from the chemical compositions of aquatic plants (by the relative ratio to carbon, oxygen, and hydrogen). The calculated PQ values range from 1.09 to 1.48 with an average of about 1.20. When the plants use ammonia as their nitrogen source, the PQ is calculated to be about 1.10 and experimentally was found to be 1.06; with nitrate-nitrogen the PQ values calculated and measured were 1.45 and 1.47 respectively (Cramer and Myers, 1948).

Contrary to the above expectations for single populations, the field data obtained in this study showed much lower PQ values. The reason for this anomaly is not clear. Low values were also found in some Florida springs by Odum (1957b). Apart from unavoidable experimental errors in the field a number of explanations are possible. The role of bacteria may significantly affect the PQ ratio since 10^7 bacteria/ml. were found by Carl Oppenheimer in the waters of the bays studied. The bacteria may be consuming CO_2 without releasing oxygen. For example, photosynthetic anaerobic bacteria, growing at the sunlit interface between mud and water, consume hydrogen sulfide and CO_2

during their photosynthetic activities and produce water instead of oxygen. There also may be diurnal changes in the kind of metabolism which may produce odd overall quotients. The correction of daytime photosynthesis with nighttime respiration may be less correct for one gas than for the other.

Another possible source of the PQ discrepancy may be the alkalinity difference between the shallow bay environments and oceanic waters; in some cases the chlorinity of the bay waters exceeded 30‰. In Figure 16 the correlation between chlorinity and

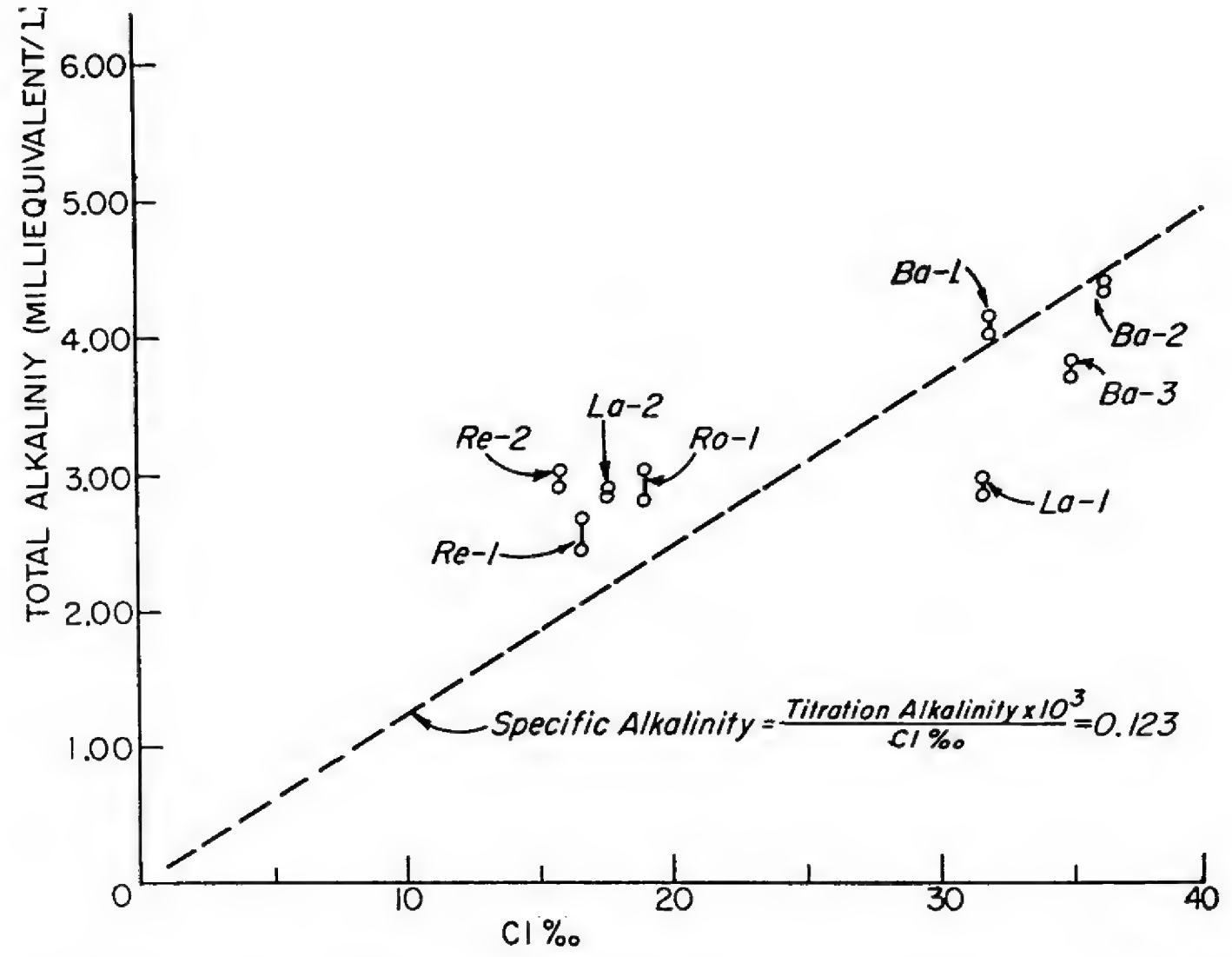


FIG. 16. Titration alkalinity as a function of chlorinity in Texas bays during summer and winter of 1957: Ba-1, Baffin Bay, July 26–27, 1957; Ba-2, Baffin Bay, Aug. 15–16, 1957; Ba-3, Baffin Bay, Dec. 22–23, 1957; Re-1, Redfish Bay, July 18–19, 1957; Re-2, Redfish Bay, Dec. 25–26, 1957; La-1, Laguna Madre, Aug. 1–2, 1957; La-2, Laguna Madre, Dec. 28–29, 1957; Ro-1 Rockport Basin, Aug. 5–6, 1957.

titration alkalinity may be observed. The ratio of alkalinity to chloride in the waters of the bays studied did not follow the pattern in oceanic waters (dotted line). Other data have indicated the variance in ion ratios of the waters of these bays as compared to that of sea water (Hood, 1952). Because of these observations, it is unlikely that the constants used in computation of the carbon dioxide components are directly applicable. The extent of this variance is indeterminable at the present time.

Calcium carbonate precipitation and dissolution from the bays would cause a marked diurnal fluctuation in alkalinity due to carbon dioxide components. Should precipitation occur, the PQ obtained should be greater than unity. Since the bays show PQ of less than unity and relatively constant titration alkalinity, it is not likely that active calcium carbonate precipitation was responsible for the odd photosynthetic quotient.

In the calculations presented above, with respect to the carbon dioxide components, it

was assumed that the effect of diffusion processes was negligible for a very low partial pressure gas involved in a dynamic biological system. It should, however, be clearly indicated that the method for detection of carbon dioxide; i.e., measurement of pH and carbonate alkalinity followed by the necessary calculations to give carbon dioxide components, does not include molecular CO_2 or that part of the system involved in direct transfer across the sea surface. If respired CO_2 is molecular carbon dioxide, then in order for this to be measured by the analytical method used, it would be necessary for equilibrium to be established. Whether this occurs in the bays is not certain. Also, it is possible for organic complexes to form such as carbamino carboxylic acids (Hood, Smith, and Jeffery, 1958) which would tend to tie up the carbon dioxide in a form not measured by the method employed. However, in the case of the carbamino carboxylic acids, it would be expected that growing plants would utilize these acids as a source of carbon in preference to the inorganic forms.

The data presented for respiratory quotient (Table 3) is as difficult to interpret as the data for photosynthetic quotients. In general, the same reasoning used for photosynthetic quotient may be applied. Additional studies of the type conducted in this study but in different environments may lead to information which would help to explain the differences observed between oxygen and carbon dioxide metabolism.

Summary

1. Diurnal measurements of pH, alkalinity, boron and oxygen were made in four contrasting Texas bays in summer and winter. The oxygen curves were corrected for diffusion and the pH data computed as total carbon dioxide. From the rate of change graphs community photosynthesis and respiration were computed for carbon dioxide changes and compared to computations based on oxygen changes.

2. In situ pH and alkalinity measurements for estimation of primary production yield values of similar order of magnitude to oxygen methods, but the difference in productivity values measured with this method and with the diurnal oxygen method needs to be explained. Photosynthetic quotients (O_2/CO_2) of 0.3–1 were observed. A better understanding of the metabolism of organisms and the physical chemistry of both carbon dioxide and oxygen in the environment will be necessary before the differences between the two methods can be resolved.

3. It is evident that calcium carbonate precipitation is not actively involved in the diurnal changes in the carbon dioxide cycle, even though the fluctuation in the carbonate ion concentration (Fig. 14) is considerable. This indirect evidence indicates that calcium carbonate precipitation and solution do not follow inorganic solubility relationships.

4. Productivities in summer are 1.5 to 2 times that in winter.

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The Chlorophyll "A" of Communities

HOWARD T. ODUM, WILLIAM MCCONNELL[1] AND WALTER ABBOTT[2]

Institute of Marine Science, The University of Texas, Port Aransas, Texas

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Introduction

Spreading over the earth in vast variety are endless ecosystems making ecological magic from sunbeams. When viewed from far above, some of the differences among systems are not visible and there is only one dark green carpet. In the uniformity of

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[1] Present address, Arizona Cooperative Wildlife Research Unit, University of Arizona, Tucson, Arizona.

[2] Present address, Dept. of Biology, Rice Institute, Houston, Texas.

greenness, therefore, one may search for some generalization in life's diversity. In this paper the ecological role of green chlorophyll is considered, and a role of chlorophyll in regulating input-output energetics is postulated. It is suggested that ecological requirements are a dominant factor in evolutionary and successional fabrication of systems controlling chlorophyll chemistry in nature.

It is presumed that machinery for purposeful adjustment of chlorophyll for the best use of light by the natural community was established through natural selection. Nonmechanistic teleology is nowhere implied.

In 1918 Willstatter and Stoll summarized the results of their studies relating photosynthesis and chlorophyll. They reasoned that photosynthesis might be proportional to the amount of chlorophyll and introduced the concept of the assimilation number, which was defined as the ratio of photosynthetic rate to the weight of chlorophyll. Although similar assimilation numbers were found by early workers among many different land plant species, differences were shown related to age, light, nutrition, and other factors. There is now an important full science of the physiology of chlorophyll in plant tissues and cells (Rabinowitch, 1945, 1951, 1956).

The attempts to use chlorophyll as a measure of the overall photosynthetic function in ecological systems began with Harvey (1934), who used visual estimates of green pigments extracted from marine planktonic communities as an estimate of the phytoplankton biomass. Following these early beginnings chlorophyll, especially chlorophyll "A", has been widely measured to characterize communities of aquatic plankton. At present a considerable literature describes quantitatively the chlorophyll in communities and cultures under many circumstances. Chlorophyll was not found to be a perfect measure of biomass of plants, but many authors have related the amount of photosynthesis to the amount of chlorophyll as Willstatter and Stoll had done (Manning and Juday, 1941; Riley, 1940; Ryther and Yentsch, 1957). Unfortunately a large range in assimilation numbers was found among different populations and conditions. Thus the use of chlorophyll as an indicator of photosynthesis has been demonstrated only in situations where the quantitative behavior of the assimilation number has been known. As used here, chlorophyll "A" is an extractable pigment fraction defined spectrophotometrically. It is recognized that more than one chemical entity may be involved.

Because chlorophyll is involved in the initial events of photosynthesis, assimilation is related to the first events of gross photosynthesis rather than to the net photosynthesis after the plant respiration has dispersed part of the energy. Little correlation was found between chlorophyll and net photosynthesis with the C^{14} method in the North Atlantic by Ketchum, Ryther, and Yentsch (Ryther and Yentsch, 1958). One can recognize the necessity for basing assimilation number on gross photosynthesis, a priori, by considering the case of a plant whose respiration balances its gross photosynthesis. There is assimilation and thus there should be an assimilation number value even though there is no net production. Rodhe, Vollenweider, and Nauwerck (1958) in lakes found that photosynthesis with the radiocarbon method was closely correlated with chlorophyll during the spring bloom period but did not correlate well in summer period. If as Ryther and associates have shown, radio-carbon methods yield net plant production, then no correlation would be expected except in the spring periods when net production and gross production are almost similar. All data and discussions here concern gross photosynthesis.

Assimilation number as used in this paper is the ratio of grams oxygen produced per hour per gram of chlorophyll "A" in any situation whether under conditions of maximum assimilation or not. As evidenced elsewhere in this paper, whole communities rarely have a light saturation level so that the natural photosynthesis and maximum photosynthesis are the same.

Unfortunately measurements of gross photosynthesis require correction for the respiration during the illumination period. The night respiration rate is usually used for the correction on the assumption that night respiration and day respiration are similar. It is understood that respiration is probably not constant (Rabinowitch, 1956: 1925), but no easy way of determining day respiration in nature is as yet available. Thus uncertainties in the assumptions underlying the use of chlorophyll are likely to be as great as present uncertainties in the chemical determinations of chlorophyll.

In the following sections measurements are presented for natural communities of contrasting types in order to extend knowledge of the chlorophyll concentration and assimilation numbers of whole communities. First some aspects of chlorophyll extraction as used for field purposes in ecology are discussed. The cannon-ball catcher analogy is introduced to permit conceptual and hypothetical generalization concerning energy adjustment. Some reasons are given for expecting total community chlorophyll to be related to gross photosynthesis whereas mere parts of the euphotic zone may not be correlated. Then data from many sources on the distribution and variation of chlorophyll are reviewed. Finally, chlorophyll data from contrasting communities are presented on an area basis with suggestions for the use of assimilation numbers to compute photosynthesis.

Acknowledgement

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Chlorophyll Methods for Ecological Purposes

Analytical determinations of chlorophyll pigments have been widely accomplished spectrophotometrically. Several authors have calibrated such determinations to permit easy analysis for chlorophyll without chlorophyll standards being available. The procedure of Richards with Thompson (1952) and Creitz and Richards (1955) has been much used by ecologists. Other spectrophotometric computations are given by Mackinney (1941).

In Richards and Thompson's procedure after samples are extracted in 90 per cent acetone, optical densities (d) are measured in a 1 cm. optical path in square cuvettes at three wave lengths (630, 645, and 665 millimicrons). Then the chlorophyll "A" is computed with the relationship in equation (1) below. The measurement at 630 millimicrons was made to eliminate effects of pigments other than chlorophyll a and b. Duxbury and Yentsch (1956) provided a nomogram for rapid computations.

$$\text{Chlorophyll "A" in mg./L.} = 16.6\ d_{665} - 2.0\ d_{645} - 0.8\ d_{630} \qquad (1)$$

Horizontal Heterogeneity

Aside from uncertainties in the procedure as described above, a number of additional sources of variation and error are involved in analyses of chlorophyll of diverse communities in nature. The difficulties of sampling from heterogeneous distributions are the most serious. For example replicate samples of adjacent bottom ooze in Laguna Madre of Texas contained 0.035, 0.078, 0.013, 0.022, 0.030, 0.021, 0.036, 0.024, 0.016, 0.018 gm./M^2 on Dec. 3, 1957; 0.081, 0.067, and 0.065 gm./M^2 on Feb. 15, 1958; and on Jan. 31, 1958, 0.270, 0.191, and 0.50 gm./M^2. Duplicate *Diplanthera wrightii* quadrat samples on Nov. 4, 1957 contained 0.163, 0.081, 0.061, and 0.027 gm./M^2 and 0.024, 0.028, 0.020, 0.020, 0.020, 0.018, and 0.022 gm./M^2 on Dec. 27, 1957. Duplicate quadrat samples of Thalassia from Redfish Bay, Port Aransas, Texas contained 0.480, 0.487, 0.190, 0.107 gm./M^2.

In addition there are difficulties with dead chlorophyll, solvents, portable spectrophotometer approximations, and varying pigment composition. In order to adapt the Richards and Thompson method to routine use in the field, several technique tests were carried out as summarized in the following paragraphs.

Non-Functional Chlorophyll

If chlorophyll of natural ecosystems is to be related to gross photosynthesis, either the non-functional chlorophyll must be eliminated from the analytical determination, or some convention must be established as to its inclusion. The presence of non-functional chlorophyll has been reported frequently in the euphotic zone (Edmondson and Edmondson, 1947; Gillbricht, 1951; Krey, 1952).

It had been suggested by Ryther and Yentsch (1957) that careful narrow band spectrophotometry could be used to eliminate active Chlorophyll "A" from non functional chlorophyll. It was reasoned that chlorophyll "A" rapidly changed to phaeophytin or other compounds with a shift in the peak of its absorption spectrum away from 665 millimicrons.

In Figure 1 are presented absorption spectra of extracts in 90 per cent acetone with fresh material and materials experimentally aged and known to be non-functional. A spectrum from marine sediments in chloroform is also included from Orr and Grady (1955). Chloroform and acetone are 3 millimicrons apart in the positions for 665 peak of chlorophyll "A" (Rabinowitch, 1951: 640). From the similarity of peaks in Figure 1 it appears that chlorophyll of living and non-living materials in nature does not necessarily differ in spectral characteristics. Certainly if non-functional and live chlorophyll cannot be separated spectrophotometrically with a narrow band pass instrument, there is no possibility of eliminating the dead chlorophyll with a broad band pass instrument suitable for portable field use.

Instead of attempting to eliminate the non-functional chlorophyll it is suggested that the convention be adopted to include all chlorophyll "A" and related substances that affect the 665 millimicron spectrum if they occur within the euphotic zone. This convention has been used in this communication. The euphotic zone is defined as the zone between the top of the plants down to the level at which visible light is extinguished to about 1 per cent of full daylight. Both on land and in water the 1 per cent level may be readily located with a photometer. On land some leaf litter may be included. It seems likely that the variation in the per cent of non-functional chlorophyll in the euphotic zone may not be as great an error as that from heterogeneous distributions and sampling.

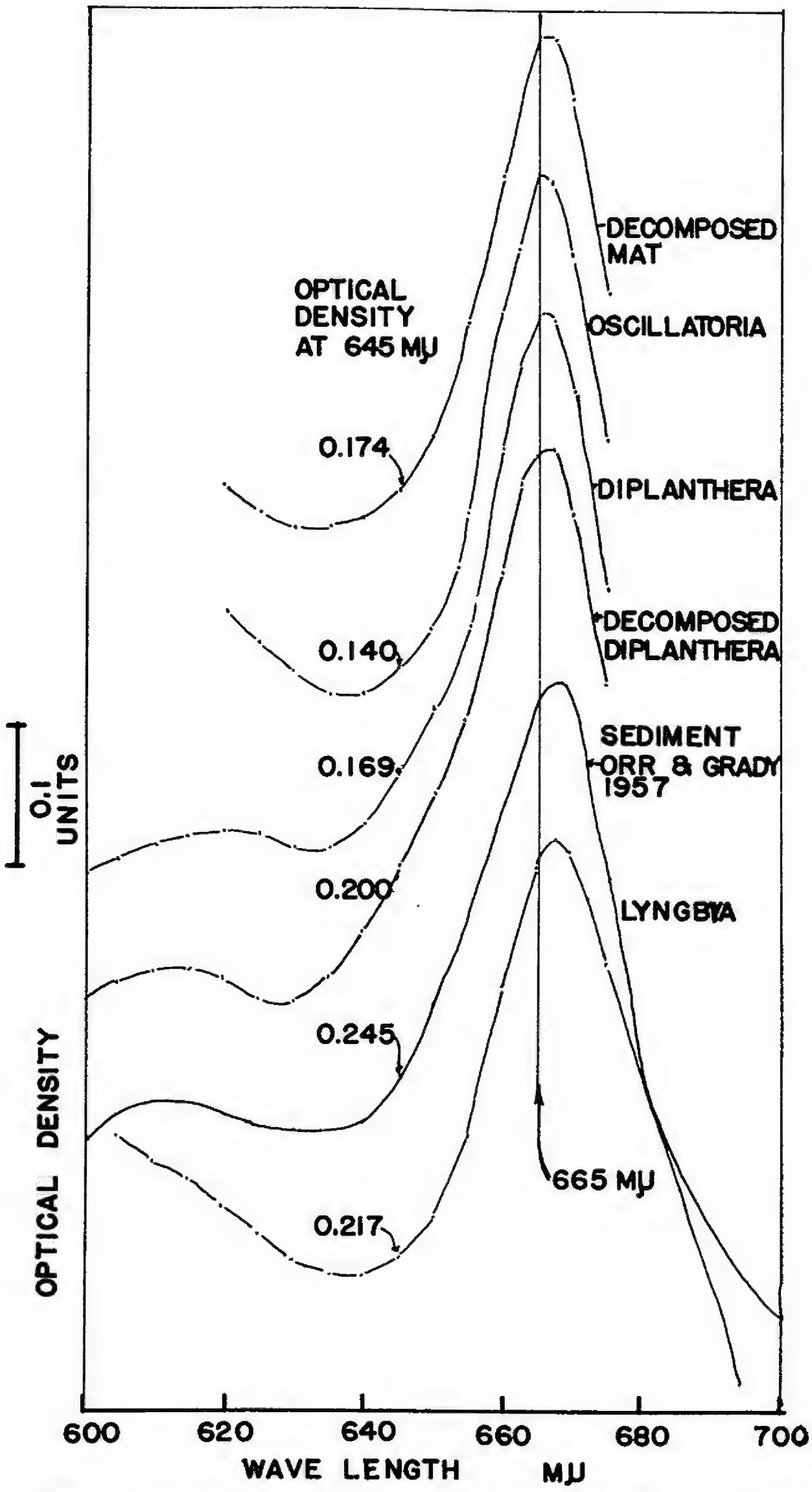


FIG. 1. Absorption spectra of living and decomposing aquatic plants. Beckman DU Spectrophotometer at slit width 0.04 mm. The peak optical density of each curve is adjusted to optical density 0.5 for comparison.

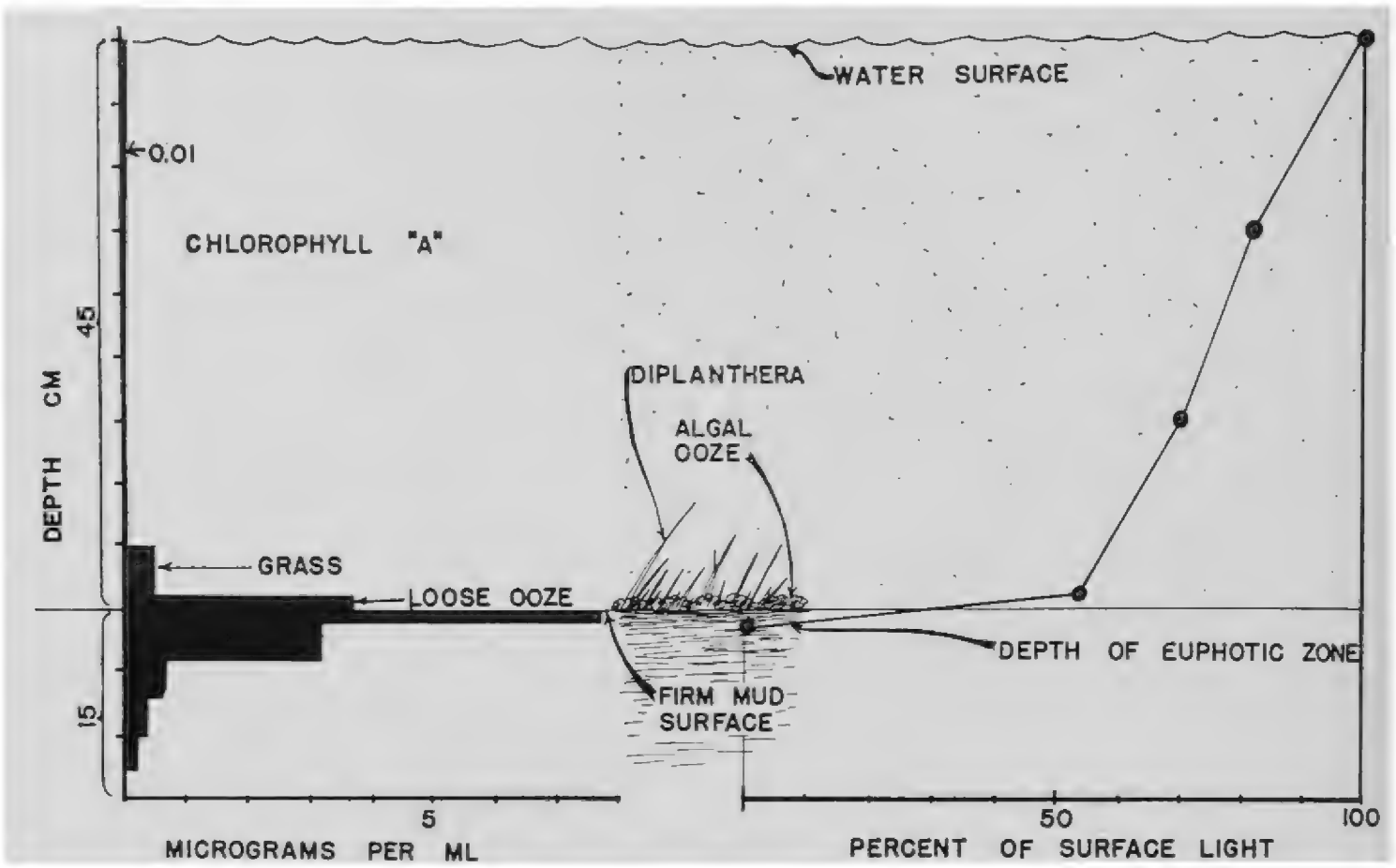


FIG. 2. Vertical stratification of chlorophyll "A" and light intensity (Dec. 29, 1957) in the shallow water and ooze of the upper Laguna Madre, Reds Fish Camp, Texas.

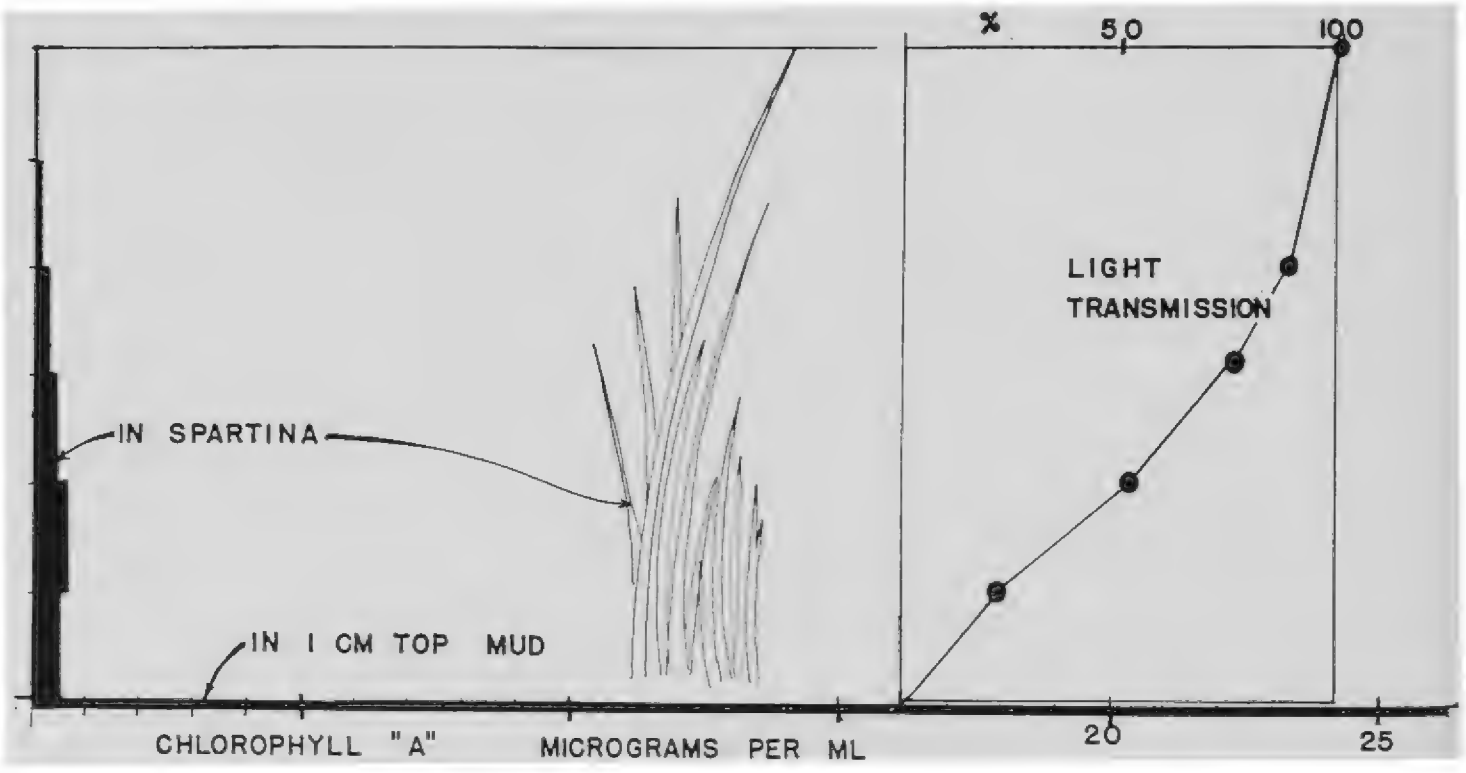


FIG. 3. Vertical stratification of chlorophyll and light intensity in the marsh grass, *Spartina sp.* and the mud surface of Aransas Bay, Texas, March 21, 1958.

Data on light intensity and chlorophyll "A" in the shallow, grassy, bay bottom of the upper Laguna Madre of Texas and in an area of sparse marsh grass near Port Aransas are given in Figures 2 and 3. The depth of the euphotic zone was measured as about 1 cm. deep into the bottom ooze. A submarine photometer was pressed into the ooze in order to determine the depth of penetration of effective light intensity. After collecting a core in a plastic pipe pressed into the mud, the core was frozen and extruded from the pipe. Then one cm. sections of the top were cut off for chlorophyll extraction. There are very large amounts of non-functional chlorophyll below the euphotic zone in the mud (Fig. 2). These deep layers are not assumed, a priori, as dead and incapable of photosynthesis, but one can assume that if no appreciable light penetrates, there is no effective

production. One must always consider the possibility of vertically migrating sediment algae, that migrate below the euphotic zone for part of the day (Aleem, 1950). Non living chlorophyll is a usual constituent of freshwater and marine sediments (Vallentyne, 1955). Large amounts of non-living chlorophyll also occur below the euphotic zone in deep layers of marine and freshwater bodies.

Chlorophyll "A" Determination from Optical Density Measurements at One Wave Length

The measurement of the optical density of chlorophyll in acetone extracts at three wavelengths is time consuming where large series are needed for meaningful averages. Comparisons of results based on measurements at 665 millicrons were made with results from measurements of three wavelengths. Widely different plant materials including blue-greens and higher plants were extracted and measured in the Beckman DU spectrophotometer. Each extract was measured at 3 wave lengths and the values computed as Chlorophyll "A" plotted against the optical density determined at 665 millimicrons (Fig. 4). The close alignment of points indicates that the 3 wave length procedure is unneces-

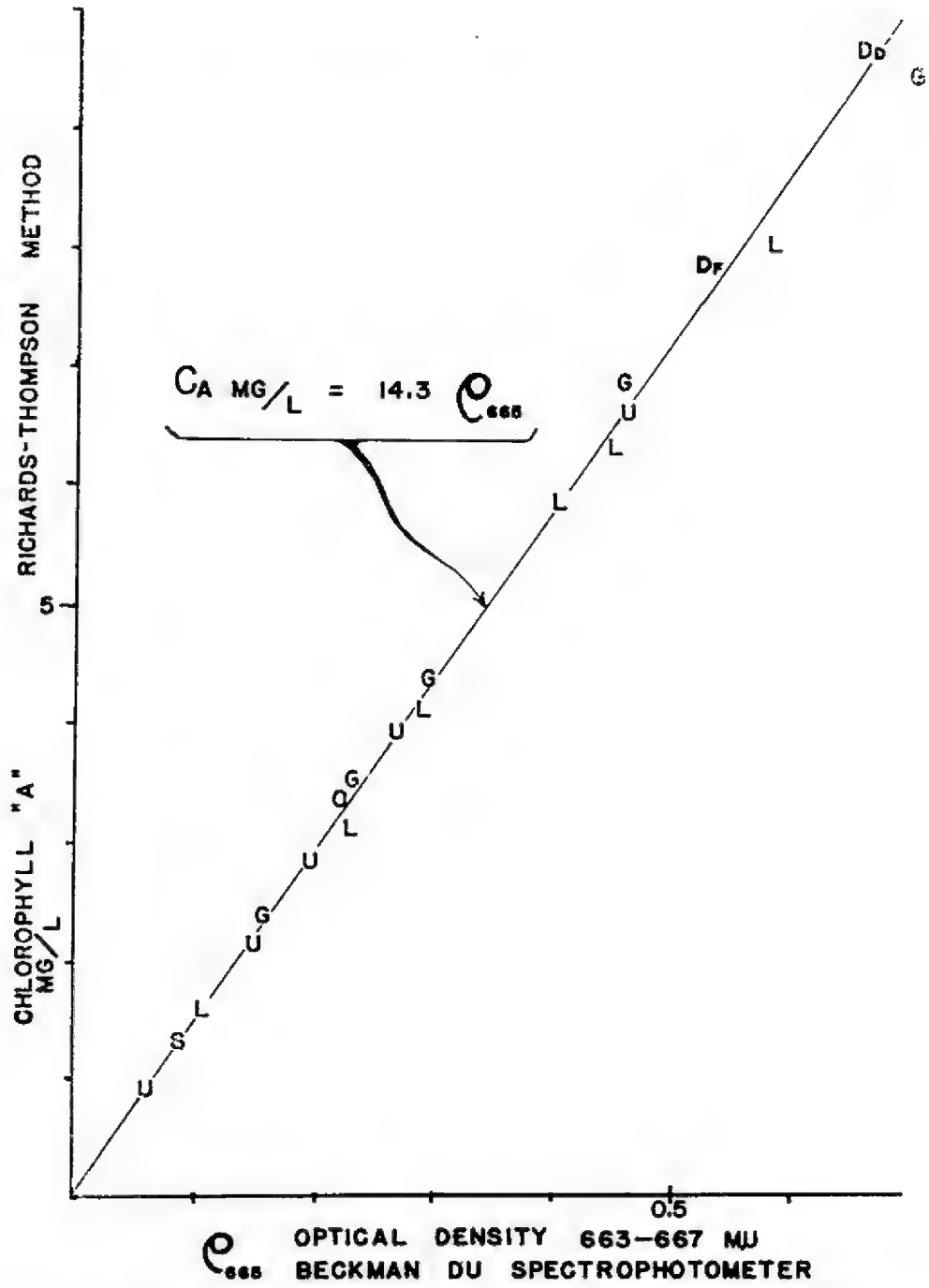


Fig. 4. Chlorophyll "A" concentration determined by the Richards-Thompson method using readings at 3 wavelengths as a function of optical density at one wavelength (665 millimicrons). Beckman DU Spectrophotometer, slit width, 0.04 mμ. U, *Ulva fasciata*; L, *Lynbya sp.*; G, *Gephortia mitchellae*: O, *Oscillatoria sp.*; D_f, fresh *Diplanthera wrightii* blades; D_s, decomposed *Diplanthera* blades; S, decomposed sedimentary material containing blue green algal mats.

sary considering the other greater sources of error. Where optical densities are read with a 1 cm. optical light path in a narrow band pass spectrophotometer, the Richards and Thompson Chlorophyll "A" procedure is abbreviated in equation (2) as follows:

$$\text{Chlorophyll A in mg./l} = 14.3\ d_{665} \quad (2)$$

Chlorophyll "A" Determination on a Portable Spectrophotometer with Broad Band Pass

The Bausch and Lomb "Spectronic 20" spectrophotometer has been found useful for determinations of chlorophyll because of portability, reliability, and relatively low cost ($240) permitting semi-field use. The width of the spectral band pass is given by the manufacturer as 20 millimicrons. Thus when the wave length is set on 665 millimicrons, light between 653 and 673 millimicrons is passing into the extract tubes. Thus the range of absorption is broad enough that the amount of Chlorophyll "B" present can affect Chlorophyll "A" determinations. Chlorophyll "B" has an absorption peak at about 645 millimicrons not far from the 653 millimicron light.

A series of measurements was made on both the Beckman narrow band pass instrument and on the broad band pass Bausch and Lomb instrument. In Figure 5 the Chlorophyll "A" figures with the Richards-Thompson method are plotted against the optical density readings at the single 665 millimicron setting on the Bausch and Lomb instrument. Data for a red, green and blue-green alga differ considerably. Readings on broad band pass instruments differ from narrow band pass measurements even when there is but one pigment present. The average per cent absorption over the 20 millimicron range must be on the average less than the per cent absorption in a 5 millimicron band pass located on the sharp peak of absorption.

Thus when the Bausch and Lomb instrument is used for field use it is desirable to convert optical density measurements into Chlorophyll "A" values with curves like those in Figure 5. A calibration graph determined for higher plants should not, for example, be used to compute Chlorophyll "A" values in extracts from red algae.

In the chlorophyll procedure of Hogetsu and Ichimura (1954) chlorophyll is converted into phaeophytin with acid. In the chlorophyll procedure of Creitz and Richards (1955) magnesium carbonate is used to prevent the decomposition of chlorophyll into substances like phaeophytin. In these considerations a shift or possible shift of the red peak of chlorophyll is involved. If a wide band spectrophotometer is used all of the compounds with peaks in this area are measured, and the conditions of handling may not be so crucial. For field use in a wide variety of types of plant material, simplicity in chemical procedure is essential. Where the largest errors are likely to be ones of sampling, rapid methods which permit replications are desirable.

Since the roles of Chlorophyll "B" and "C" in photosynthesis are not adequately known, it is not possible to state whether or not plants with much Chlorophyll "B" or "C" will have a different assimilation number relative to Chlorophyll "A" in comparison to plants without these pigments. Assimilation numbers in this paper are computed relative to Cholorphyll "A" only.

Notes on Extraction

The extraction of Chlorophyll "A" from widely divergent materials for ecological purposes, requires a variety of extraction methods. Large, leafy plant itssues are passed through a meat grinder, slurried in water, aliquoted, partially dried, and extracted with

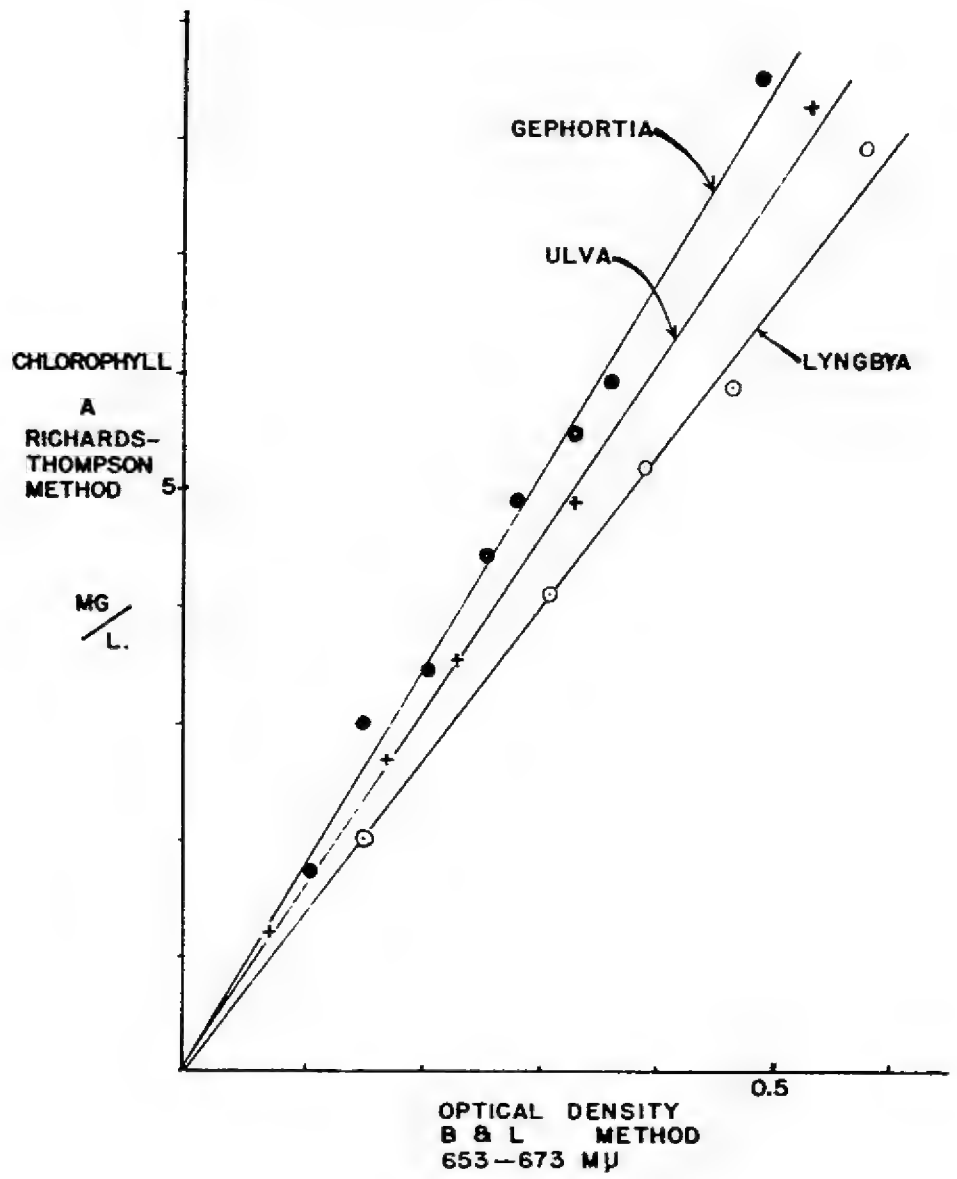


FIG. 5. Chlorophyll "A" determined with the Richards and Thompson method on the Beckman DU spectrophotometer as a function of optical density at 663 millimicrons and 1.17 cm. light path on a Bausch and Lomb "spectronic 20" spectrophotometer. *Ulva fasciata*, a green alga; *Gephortia mitchelae*, a red alga; and *Lyngbya major*, a blue-green alga.

90 per cent acetone. Discs from rain forest leaves were punched, bruised, placed in 10 cc. acetone (90%) in vials, and extracted completely in 24 hours in a refrigerator without further grinding. Some plankton samples on millipore filters extract readily without mechanical damage to cells (Creitz and Richards, 1955). Other algae require grinding in mortar and pestle with clean sand. Corals and calcareous algae were cut with hacksaw and ground in a mortar.

Rocks in streams were extracted by immersion in pans of acetone accompanied by brushing by McConnell (1958) and in class sampling work at Duke in 1956. Freeze drying of leaves was effective where preservation was necessary and where greatest accuracy was desirable.

Some algae are sufficiently bruised in a Waring blendor for subsequent extraction. Others resist extraction. Species of *Prasiola*, *Ulva*, *Cladophora*, *Thalassia*, *Diplanthera*, *Phormidium* and *Enteromorpha* were especially resistant. With larger tissues, observation of the residual color may be used to ascertain if most of the extraction has taken place. With tiny plankton cells on a millipore filter, the lack of extraction may be readily overlooked. In one extraction involving a species of *Chlorella*, only a small fraction of chlorophyll was removed from the filter residue until grinding was done with sand.

Extraction is made with 90 per cent acetone. If 100 per cent acetone is used to dissolve millipore filters, a part of the filter goes into solution which precipitates as a milky turbidity later when the solution is adjusted with water to 90 per cent acetone. Ideally

final extracts are in 90 per cent acetone. Final stages of extraction are usually carried on for 24 hours in a refrigerator in the dark.

Validity of Richards and Thompson's Procedure for 90 Per Cent Acetone

In developing the chlorophyll assay method (equation 1 in this paper) Richards with Thompson (1952) cite the work of MacKinney (1941) and Zscheile, Comar, and MacKinney (1942) and adopt extinction coefficients for use in 90 per cent acetone solutions. Richards with Thompson (1952) prepared Chlorophyll "A" from *Macrocystis* with chromatographic methods and used the coefficients of the previous authors for determining the grams of chlorophyll represented by the extraction. MacKinney made measurements at 663 millimicrons whereas Richards used his new curve to determine absorbancy at 665 millimicrons. In actuality, the extinction coefficients reported by Zscheile and co-workers and MacKinney are for 80 per cent acetone solutions of pigments. The effects of changes of solvent on the spectrophotometric properties of plant pigments have been widely discussed elsewhere (Franck and Loomis, 1950; Rabinowitch, 1951). A series of experiments was run by Walter Abbott to test the effect on absorbance of a change of solvent from 80 per cent to 90 per cent with pigments from terrestrial plants. (This was not a test of extractability, but a test of the basis of Richards and Thompson's equation.)

Small portions of fresh leaves from a variety of plants were extracted with 10 ml. of neutral, redistilled reagent grade acetone. Extraction was carried out in the dark at 5° C. When extraction was completed, two 4 ml. aliquots were withdrawn. With a microburette, these were adjusted to 80 per cent and 90 per cent acetone contents by addition of distilled water. Correction for nonideal behavior of acetone water mixtures was made from an empirically determined chart of volume relationships. Samples were then cooled and stored briefly in the dark until spectra could be scanned on the Beckman DK recording spectrophotometer. Data from these measurements are in Table 1.

Table 1

Absorbance Values

(Optical Density in 1.0 cm. Light Path)

Species	663 mu		645 mu		630 mu	
	80%	90%	80%	90%	80%	90%
Catalpa bignoniodes	0.600	0.649	0.264	0.279	0.170	0.166
Quercus phellos	0.441	0.474	0.199	0.219	0.113	0.124
	0.568	0.581	0.258	0.268	0.145	0.147
Rhus glabra	0.410	0.434	0.176	0.189	0.100	0.103
	0.664	0.718	0.303	0.332	0.167	0.189
Celtis occidentalis	0.538	0.564	0.244	0.252	0.140	0.140
	0.952	0.956	0.427	0.447	0.248	0.228
Ulmus americana	0.286	0.302	0.131	0.135	0.082	0.082
	0.252	0.356	0.133	0.154	0.084	0.088
Quercus virginiana	0.890	0.972	0.333	0.344	0.189	0.188
Juniperus mexicanus	0.366	0.502	0.164	0.207	0.085	0.117
Cercis canadensis	0.517	0.558	0.175	0.209	0.082	0.101
Unidentified seedling	0.568	0.581	0.227	0.226	0.110	0.107

Accompanying the change of solvent from 90 per cent acetone is a 6 per cent lowering of absorbance at 663 millimicrons and at 645 millimicrons. Data taken by the Richards and Thompson method should be corrected by multiplying absorbances at 663 millimicrons and 645 millimicrons by 0.94. Equation (2) above thus modified becomes equation (3) below:

$$\text{Chlorophyll "A" in mg/1 of 90\% acetone} = 13.4\ d_{665} \quad (3)$$

With the Bausch and Lomb broad band pass instrument, however, the composition of the extract is not so important since part of the solvent effect is a change in wave length of the peak of the spectrum. McConnell (1958) found relatively minor effect of changing water composition.

Steady State Energetics of Input-Output Systems in Which the Input Energy Arrives as Packets of Fixed Energy Content; The Cannon-Ball Catcher

In order to better understand the energetic coupling of biochemical machines to the steady inflow of photons of light, it is convenient to describe the cannon-ball catcher (Fig. 6). Although the machine is an analogy, its energy aspects are thought to be similar to those of primary production systems. It is possible to erect hypotheses which account for the behavior of input-output systems containing chlorophyll with respect to light, temperature, nutrients, and other factors. That the behavior of chlorophyll adaptation seems logical when compared with a cannon-ball catcher is at least an aid to the memory. In the discussion that follows the behavior of chlorophyll is related to mechanisms of self regulation believed to exist in plants at a higher level of organization than single reactions of photochemistry and photosynthesis.

The cannon-ball catcher machine is a coupled input-output system like those described in a previous paper (Odum and Pinkerton, 1955). Energy arriving in the form of cannon-balls is caught by cups on a turning wheel of the cannon-ball catcher. The input energy system thus receives a steady flow of energy in discontinuous similar packages. After catching a ball, a receptor to be used again must be revolved through a cyclic process requiring a discrete time. The input system is geared by a pulley system and a fly wheel to a machine for doing work. Therefore, a discontinuous energy input drives an output that may have a more regular power distribution with time. A review of the possible kinds of biochemical reactions by which such input-output systems might function is given by Strehler (1958).

There are several similarities between a cannon-ball catcher and a photosynthetic machine. A plant receives discontinuous photons just as the catcher receives cannon-balls, and is geared to a chemical machine that produces organic, synthetic work. The number of cups per machine is comparable to the concentration of chlorophyll per chloroplast. A cyclic biochemical process is necessary for maintaining chlorophyll "A" in receptive state (see flashing light research: Rabinowitch, 1956: 1433) just as the cups on the wheel must be revolved for reuse. As discussed previously (Odum and Pinkerton, 1955) maximum power output is gained with a particular and optimum force adjustment between input and output systems. It is likely that plants contain mechanisms for maintaining optimum adjustments, and these are established by natural selection.

Consider a situation with a steady influx of cannon balls. The steady torque developed

by the impinging balls can be varied by changing the number of cups on the catcher wheel. With more cups more balls are caught. In this way the input drive can be adapted for a given output load so as to provide the maximum power. The rest of the cannon-balls can pass uncaught to be accepted by another catcher machine below.

Similarly in photosynthesis one can imagine that the number of receptive chlorophyll molecules provided can be controlled in order to maintain the ideal photochemical drive to the respiratory system. Changes in light or in factors affecting respiratory system rates are likely to be accompanied by changes in chlorophyll in order to maintain the adjustment within the chloroplast. Such adjustment prohibits acceptance of too many or too few photons. Conservation of photons not only maintains proper load ratios in the immediate biochemical system but contributes to the maximum output of cells just below.

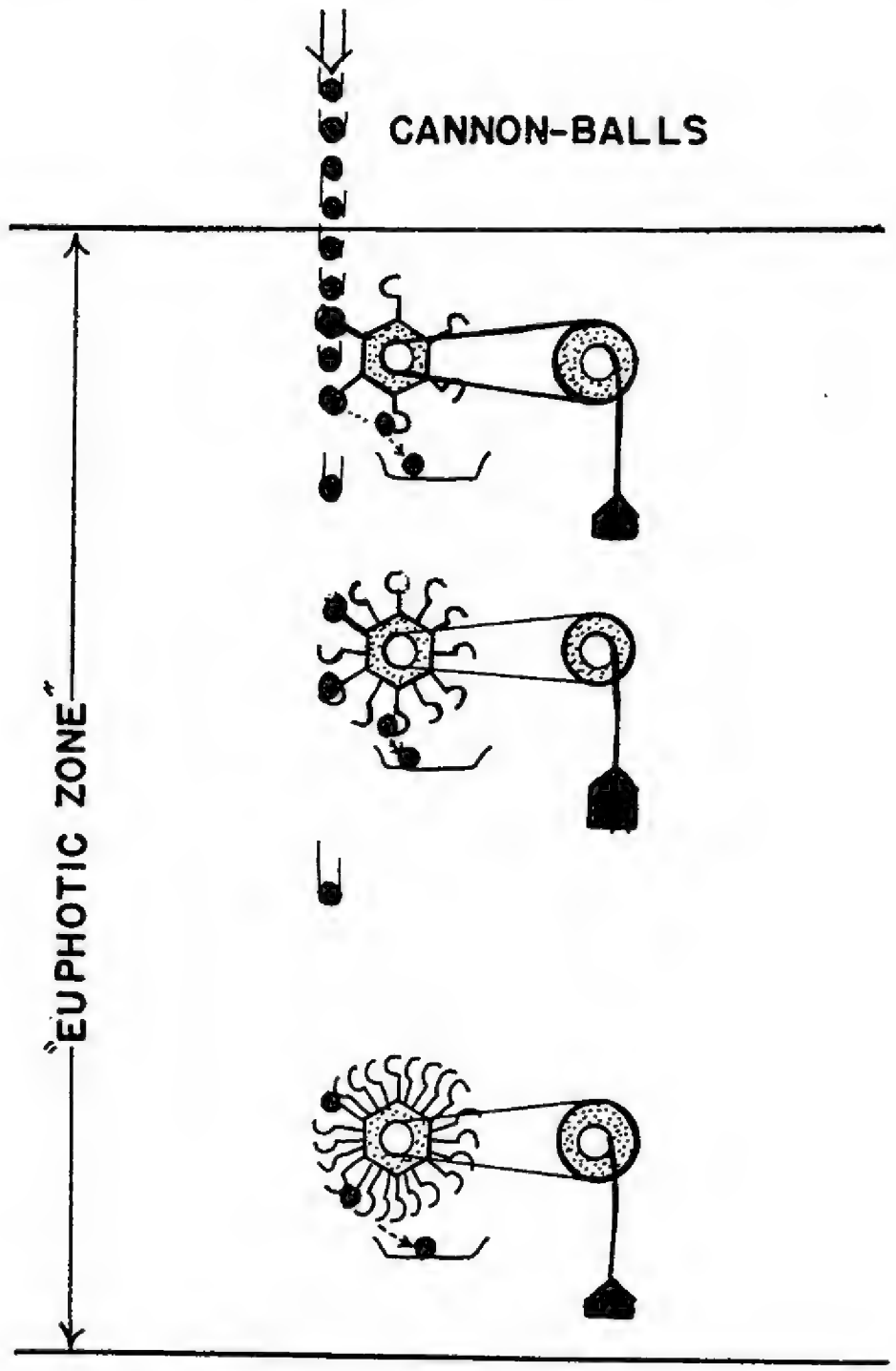


FIG. 6. Three cannon-ball catcher machines in vertical sequence. The upper machine is adapted to the area of great flux of cannon-balls because relatively few cups are protruding; the lower machine is adapted to the area of few cannon-balls with a large number of cups in position.

According to the theory of energy adaptation, outlined in the text, successfully surviving photosynthetic systems adapted in nature have mechanisms to change number of cups in order to adapt to the rate of energy influx and so as to develop maximum power output of the entire population throughout the euphotic zone.

The total yield of the whole euphotic zone is thus higher. Maximum yields are possible if a multi-layered reception system is active.

If the theory of optimum input-output adjustment of chlorophyll is correct, then the chlorophyll fluorescence as an input energy flow meter (Katz, 1949) is likely to be maintained in fairly constant ratio to photosynthesis under adapted circumstances. A correlation of the fluorescence of live chloroplasts and photosynthesis does exist (Rabinowitch, 1951: 819; Brugger, 1957).

The fluorescence of living chlorophyll systems may have some analogous similarity to the loss of energy that occurs when a cannon-ball strikes the cups of the catcher machine. Both phenomena are likely to be accentuated when the cycles of the receptive material (cups or chlorophyll) are being retarded and are not dispersing energy at optimum speed. Katz (1949) found increased fluorescence with artificially retarded photosynthesis.

Discussion of chlorophyll, light, and other factors follow with reference to energetics and input-output systems.

The purpose of the cannon-ball picturization is to make clear the hypothesis that photosynthetic systems in order to maintain maximum power output can regulate the input power by regulating the chlorophyll.

Summary of Ecological Factors Affecting Chlorophyll and Assimilation Number

Reports from the literature on the spatial and temporal patterns of chlorophyll in natural communities are not uniform. Nor do the data from the experimental literature at first suggest simple relationships between environmental factors, chlorophyll, and assimilation. In the following paragraphs an attempt is made to summarize and account for the adaptive behavior of systems containing chlorophyll.

Light Intensity and the Chlorophyll Concentrations in a *Part* of a Community

Consider only plants growing under conditions of illumination to which they are adapted for effective competition. Such adaptation may be in the laboratory or outdoor situations. In adapted condition the chlorophyll of single leaves, cells, and other community parts tends to be diminished as the chloroplasts adapt to increasing light intensity (See various authors cited by Rabinowitch, 1956: 1261). However the effectiveness of adapted chlorophyll for photosynthesis (i.e., assimilation number) increases with light intensity. (See examples cited by Rabinowitch, 1957: 1262). With less chlorophyll per cell a larger part of the incident light passes through to the next layer of plants so that the total energy absorbed for photosynthesis in the top layer may be less. Consequently single cells or leaves may have lower, equal, or greater total photosynthesis in brightest light. It may be a misnomer to refer to diminished output of naturally adapted cells in bright light as saturation in any sense of malfunction. The effect of adaptation to intense light is to increase the assimilation number of the top cells in spite of decreasing chlorophyll concentration. In a yellow variety of *Sambucas* Willstatter and Stoll (1918) measured an assimilation number of 84 gm./gm./hr. In contrast, shaded cells of a community possess higher chlorophyll concentrations and lower assimilation numbers. At light intensities for maximum photosynthesis of single

cells, assimilation numbers of 7.4 gm./gm./hr. (range, 4 — 12 gm./gm./hr.) are found (Ryther and Yentsch, 1957).

These relationships of assimilation number, chlorophyll, and light have been shown by many authors. For example, Phillips and Myers (1954) presented a graph for *Chlorella* which shows diminishing chlorophyll per cell with adaptation to greater light intensity. Ichimura (1958) reports data on lake plankton in field conditions with rising assimilation numbers correlated with increasing light intensity for three seasons. Assimilation numbers were about 1 gm./gm./hr. with 3 per cent light rising to 7 gm./gm./hr. at 60 per cent light.

The adaptation found for chlorophyll and assimilation in bright light may be compared to the cannonball-catcher in a zone of numerous flying cannonballs. In order that the same torque be exerted upon the output machinery, it becomes necessary to diminish the number of cups on the wheel. An overloaded system runs too fast for most effective use of the energy. By reducing the number of cups the top machine works at optimum and the uncaught balls pass below to the next cannonball machine for effective use there. The decrease in number of cups in this situation may be compared to decrease in chlorophyll in bright light. With plenty of cannonballs for the available cups, there is a large work output per cup just as there is a large assimilation per unit chlorophyll.

The large chlorophyll content of cells adapted to the shade may be compared to the numerous cups on the cannonball-catcher. Many cups are needed to maintain enough power output for survival. With few balls received the output work per cup is small just as the assimilation per unit chlorophyll is small in the shade. Efficiency is large in a slowly turning wheel because there is a greater potential energy difference maintained between incoming and acceptor energy states. The efficiency of the slowly turning wheel may be compared to the high efficiency that occurs with low rates of assimilation of plants adapted and operating in the shade (Nihei, Sasa, Miyachi, Suzuki and Tamiyo, 1954).

Gessner (1949) adapted lake plankton for five days in light and dark conditions. The plankton initially had an assimilation number of 1.4 gm./gm./hr. At the end of the experiment the shaded plankton had an assimilation number of 0.1 gm./gm./hr. whereas the plankton in bright light had an assimilation number of 5.8 gm./gm./hr.

Marshall (1956) showed relative increase of marine plankton chlorophyll in bottles in shade relative to bottles at the surface. Manning and Juday (1941) found higher assimilation numbers in hypolimnetic plankton. Sargent (1940) showed twice as much chlorophyll in shade adapted *Chlorella* as in light adapted algae, although the light adapted algae had the greatest yields. He reviewed the work of five earlier authors with similar results.

In Sargent's work the chloroplasts in the sun had less chlorophyll present. Gessner (1955) described thinner chloroplasts in *Spirogyra* in light adapted plants. Movements of the chlorophyll and chloroplasts so as to transmit more light under bright light conditions are summarized by Rabinowitch (1951:681).

Light Intensity and Chlorophyll in the Whole Euphotic Zone of a Community

The total chlorophyll which develops under a square meter tends to absorb most of the available light. A thick zone of chlorophyll may develop which is light adapted at the

top and shade adapted below. The greater the light intensity is at the top of the community the greater the total amount of chlorophyll which develops within the euphotic zone. For a whole lake Ichimura (1958) found increasing assimilation numbers as chlorophyll increased.

The chlorophyll per unit area thus increases with light intensity under adapted condition even though the chlorophyll per cell may decrease in the upper layers. An apparent paradox results. Communities adapted to bright light may seem pale from above and yet may contain more chlorophyll. The greenest appearing communities are not necessarily the most photosynthetic or the greenest in extraction. Pale appearing communities, however, do not necessarily have additional chlorophyll below, for there are other limiting factors such as nutrients.

The effectiveness of the total chlorophyll of the whole euphotic zone increases with incident light intensity. Increase of light intensity causes bright adapted cells with high assimilation numbers to develop on top of and in addition to the cells present under lesser light intensities. Thus the overall assimilation number increases with incident light.

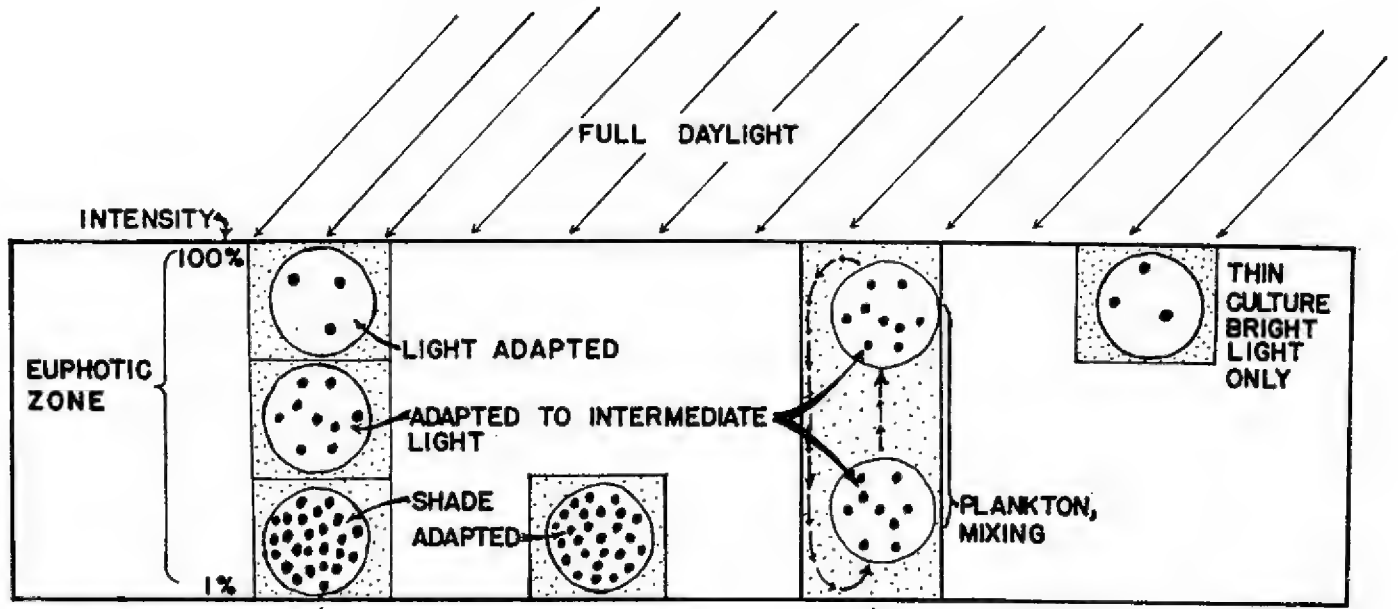
Since in whole communities both chlorophyll and assimilation number increase with light intensity, total photosynthesis increases with light intensity even under conditions of full daylight. The whole zone therefore in photosynthetic response to bright light differs from the behavior of single cells, leaves, or small plants. Parts of communities have optimum light intensities for maximum photosynthesis. See numerous examples in Rabinowitch (1951:964) and Gessner (1955). Whole naturally adapted communities have maximum photosynthesis at maximum light intensity. Examples of communities (whole euphotic zone) without maxima in their photosynthetic curves (per area) with light are: mass algal culture (Burlew, 1953: 17); Silver Springs (Odum, 1957); pine tree (Kramer, 1958: 163); aquatic plants (Gessner, 1955: 86); marine waters (Marshall and Orr, 1929; Jenkins, 1937; Ryther, 1956b); *Cabomba* (See Rabinowitch, 1951: 968); lakes (Ichimura, 1958); Lake Erie plankton in seasonal comparisons (Verduin, 1956); and surface algae (Manning, Julay, and Wolf, 1938). Takeda and Maruta (1956) found light saturation in individual rice plants but not in communities of rice plants.

In plant cells in which there is an optimum light intensity for maximum photosynthesis, a midday depression in production may occur (Rabinowitch, 1951:873). In an adapted community with a full depth of chlorophyll, midday depression is not expected. Any tendency for saturation of surface cells is more than compensated for by additional photosynthesis of the deeper cells receiving light only during the brightness of midday.

Because shaded communities are more efficient (not more productive) than light adapted zones, assimilation and assimilation numbers do not diminish on cloudy days as much as the light intensity. Steeman-Nielsen (1954), Verduin (1956), and Edmondsen (1956) have reported smaller deviation in community photosynthesis than expected from changes in light intensity. Community efficiency increases as light intensity diminishes (Wassink et al., 1953; Odum and Hoskins, 1958).

Four Types of Chlorophyll Adaptations to Light by Producer Systems

The general principles concerning chlorophyll states and light in plant communities can be summarized by considering whole natural communities and laboratory experiments as belonging to one of four types pictured in Figure 7. The difficulty encountered



TOTAL AREA CHLOROPHYLL "A" GM/M^2	0.4-3.0	0.001-0.5	0.02-1.0	0.01-0.60
COMMUNITY ASSIMILATION RATIO $GM/GM/HR$	0.4-4.0	0.1-1	1-10	8-40
EFFICIENCY OF VISIBLE LIGHT ABSORBED %	1-8	10-30	1-5	0.1-3
PHOTOSYNTHESIS GROSS $GM/M^2/DAY$	1-60	0.01-1.0	0.5-30	0.5-10

FIG. 7. Four types of chlorophyll adaptations to light by producer systems. The concentrations of chlorophyll are indicated diagrammatically by the density of dots in the circles. Estimates of chlorophyll, assimilation number, efficiency, and community photosynthesis are derived from Table 2 and from the literature.

in recognizing light adapted patterns in nature is attributed to the interplay of other factors on the vertical distribution of chlorophyll.

1. *Stratified community*. There are light and shade adapted portions. Chlorophyll per cell increases downward. All of the incident light is effectively used. Assimilation number decreases downward but the overall assimilation number of the community is high. The overall efficiency of photosynthesis is also high. The total chlorophyll per area is large but may not appear so from the top view. Such communities are the most productive of any yet measured. Forests and benthic communities are examples of this type. Some stratified, quiet waters develop vertical stratifications of planktonic algae with similar patterns.

2. *Shaded Community*. A community developing and becoming adapted to low light intensity may be considered to be the same as the lower portion of a stratified community in full daylight. In other words, the shaded community lacks the light adapted parts. It is relatively high in chlorophyll concentration but has less than the stratified type although it may appear much greener. With lower light intensities efficiency is greater but with so little light the total photosynthesis is less. The excess chlorophyll needed to gather light in shaded conditions is not in effective continual use and the assimilation

numbers are small. Such communities may occur in winter seasons, in caves, and in most laboratory work where light intensities are rarely as bright as full daylight. Many misleading ideas have developed concerning nature from work with shade adapted communities. Many popular writers overestimated the possible yields of algae by considering as representative the high efficiencies found at low light intensity.

3. *Mixing Community.* In turbulent upper waters of lakes and oceans at some seasons, the principal producers are moved up and down and are subjected to alternating conditions of shade and light. Cells move from full daylight to half daylight in a matter of a minute or two where mixing is effective. (See discussion of the diffusion of oxygen (Odum and Hoskins, 1958). Waters in the upper zones of aquatic environments also receive flashing light due to wave effects at the surface in diffracting and reflecting light. Especially in the sea such cells cannot become adapted to either shade or bright conditions. It is possible that plankton cells of this type are adapted to intermediate light. As might be expected, such cells have intermediate chlorophyll concentrations and assimilation numbers (Table 2 and Fig. 7). If the euphotic zone is spread over any appreciable depth, the water absorbs a large proportion of the potentially usable light as Steeman-Nielsen (1957) has discussed. Such communities may thus receive less total light, develop less total chlorophyll per area, and yield less total photosynthesis. Ryther (1956a) was unable to find much light and shade adaptation in *Dunaliella* in contrast to the adaptation in other species found by many workers. Ryther found assimilation numbers of only 1–5 gm./gm./ hr. in contrast with higher numbers in other data for light adapted cells. However, no adaptation was attempted above 1500 ft. candles whereas daylight is usually greater than 10,000 ft. candles. Whether usual plankton algae are capable of becoming light and shade adapted cannot yet be generalized.

In a rain forest in the intermediate depths, light is rather uniform due to the scattering of light by the leaves (unpublished data of Odum, Abbott, and Selander). Such forest leaves may also be adapted to intermediate light intensities. As the leaves are rustled by the breeze on bright days, flecks of bright sunlight momentarily illuminate the lower layers. Thus forest leaves on a sunny day are exposed to considerable variation of incident light intensity, and adaptation to one light intensity may be difficult. Steeman-Nielsen (1957) presents a discussion of light and chlorophyll in forests and waters.

4. *Thin culture with all bright light.* In many laboratory cultures especially those with lights inside the containers, there is no part of the system where there is shade. Such cultures, which are never allowed to get so dense as to produce their own shade, may be visualized as the upper part of a full stratified community. Unfortunately, generalizations have been made about such cultures without realization of their specialized nature. One may overestimate potential yields if one extrapolates with the high assimilation numbers of light adapted cultures.

A bright adapted community has low concentrations of chlorophyll per volume of cells and has very high assimilation numbers. Efficiency of use of the light absorbed is low at high light intensity. Total area based photosynthesis may be higher than in the shade adapted community but is less than in the two types of communities that represent full euphotic zones. Such cultures are particularly misleading about chlorophyll since the assimilation numbers are much higher than in full depth communities (20 gm./gm./hr.; Ryther, 1956a). Such communities occur in nature where only thin vegetation can develop sometimes on surfaces of rocks, water, or in new colonization. Agri-

culture is often of this type. Sunflowers have high assimilation numbers (8–16 gm./gm./hr.; Willstatter and Stoll, 1918).

Limiting Material Requirements and Chlorophyll

Consider next plants growing with adequate light but sub-minimal rates of supply of the materials needed for photosynthesis and growth. The literature of plant physiology (Hill and Whittingham, 1955, for example) and plant ecology (Harvey, 1955, for example) are full of cases in which limiting factors are demonstrated. Chlorophyll concentrations diminish when plants adapt to maintain minimal existence in limiting environments. Physiological studies indicate that subminimal amounts of different limiting factors including iron, nitrogen, potassium, magnesium, and water induce lowered chlorophyll as summarized by Rabinowitch (1945: 427; 1956: 1267). The operation of nutrients in stimulating increase of chlorophyll in whole community systems also has been frequently noted. For example S. Conover (1956: 85) showed the effects of nutrients on chlorophyll of plankton populations in bottles, and Edmondson (1955) showed increased chlorophyll with fertilization in a tank. No attempt is made to separate instances where the increased chlorophyll is within cells already existing from those where new cells form.

If the output machinery is limited by some factor, a reduction of input torque is necessary to maintain the proper load ratio and to allow energy to pass to lower levels of the community where limiting conditions are possibly equal or less restrictive. The rate at which energy is entering may be diminished by the elimination of some of the receptors in each machine. In the machine the decrease in receptors is an adaptation to the mechanical requirements of the input-output gearing. The disappearance of chlorophyll in environments unfavorable for photosynthesis need not be described as pathological in plants surviving in such conditions, for the diminished chlorophyll may be an adaptation of input to the externally limited rates of output for purposes of economy. Just as the output per cup remains high so in these limitations the assimilation per unit chlorophyll remains high. The high assimilation numbers of yellowing autumn leaves (Willstatter and Stoll, 1918) may be from a diminishing supply of raw materials at the leaf site.

Many studies have related the higher chlorophyll content of generally rich eutrophic waters to high nutrient levels (Deevey, 1940; Ichimura, 1956). However, some of these studies accentuate the lesser chlorophyll of oligotrophic waters by expressing data on a volume of water basis. Thus clear water has a deeper euphotic zone and less chlorophyll per volume even when chlorophyll per area is the same. Such regional comparisons should be made on an area of community basis.

The nutrient factor is affected by temperature. At high temperatures there is a rapid regeneration rate in respiratory systems of the community so that a steady supply of nutrients is not as important.

Temperature, Tissue Size, and Chlorophyll

There are two factors which affect chemical reaction rates and as a result affect the chlorophyll content of communities. First consider temperature.

Although the initial photochemical events of photosynthesis are physical in nature and little subject to temperature, most of the photosynthetic machinery is biochemical,

metabolic, and made of reactions which follow laws of chemical reaction rate. As the temperature rises, the rates of reaction and recycling of materials increase. Materials are released by respiration more rapidly also. At high temperatures, therefore, less mateials are needed for the same flux of energy because materials are reused more often. In photosynthesis chlorophyll is connected to an action and recovery cycle that is chemical in nature, and its synthesis is chemical. Consequently, at higher temperatures less chlorophyll may be needed at any instant because of the greater possible turnover rate. Even though the chlorophyll functions in a temperature independent photochemical action, the amount of chlorophyll is regulated by a temperature dependent system in order to maintain optimum input-output adjustment. Assimilation numbers may be larger (Rabinowitch; 1956: 1272). Willstatter and Stoll (1918) found slight increase in assimilation number from 25° C. to 30° C. Myers and Kratz (1955) found less chlorophyll developed at higher temperatures in *Anacystis*. With less materials to maintain, cells may be smaller for the same job at high temperatures. Next, consider tissue size as a factor.

It is now known in plants that in photosynthesis as well as in respiration smaller cells have greater turnover (Margalef, 1957; H. T. Odum, 1956; E. P. Odum, Kuenzler, and Blunt, 1958). The metabolism per gram inversely varies approximately as the $\frac{1}{3}$ power of the linear thickness of the tissue. It has been postulated that diffusion properties are responsible for the greater metabolic rate of smaller cells because the power of diffiusion per gram to carry materials into and out of the cell varies as the $\frac{1}{3}$ power of the thickness. In any case the smaller the plankton cell or the thinner the leaf tissue, the more rapid is the possible metabolism per cell. In small cells with more chemical respiratory turnover per gram, more chlorophyll per gram (or per volume) is necessary to maintain proper input torque than in large cells, but as in temperature effects, it may again be postulated that conditions permitting rapid turnover will similarly permit the cells to maintain higher assimilation numbers and less chlorophyll for the same photosynthetic flux. The respiratory output rate by this hypothesis controls the adjustment of chlorophyll for proper input-output stress.

If these postulations are correct, higher assimilation numbers may be expected in smaller cells and at higher temperatures. In terms of input-output systems any modifications of the circulating machinery which permits a more rapid turnover, will permit fewer receptors to catch the same number of energy units.

In Table 2 are presented data on chlorophyll in communities. There is a tendency for higher assimilation numbers and smaller chlorophyll contents per area in plankton communities than in communities made up of plants with thicker tissues. In *Chlorella* smaller individuals have more chlorophyll per gram and greater assimilation numbers (Tamiya *et al.*, 1953). In the Laguna Madre of Texas (Table 3) assimilation numbers are higher in the plankton than in the benthic plants beneath.

Chlorophyll in Partially Heterotrophic Plants

In completely heterotrophic plants chlorophyll may be absent, but in some partially heterotrophic organisms there may be chlorophyll based nutrition as well as heterotrophic based energy intake. At the base of a growing aquatic plant, blades in the tissues recently formed from meristematic growth, and in *Euglena* cultures placed in the dark, there are cells which may have photosynthetic capacity when placed in the light at a later time, but which are living off imports of organic food. Such tissues apparently have

TABLE 2

Chlorophyll and Assimilation Number in Communities

	Euphotic Zone Chlorophyll "A" Gm./M.^{2}	Assimilation[a] Number Oxygen gm./gm./hr.
PLANKTON COMMUNITIES (Not including bottom plants)		
Fertilized tank, marine, 1.5 M deep (Edmondson and Edmondson, 1947)	0.030	7
English Channel, 70 M deep (Jenkins, 1955)		
Summer and winter	0.20	....
Spring blooms	1–3	....
Long Island Sound (Riley, 1956; Conover, 1956)	0.1–0.6	1–3
Phosphorescent Bay, Lajas, Puerto Rico, 3.7 M deep		
January 23, 1957	0.033	4
Baffin Bay, Texas, 1–2 M deep, turbid hypersaline	0.043–0.066	2
North Sea Fladen Ground, May bloom (Steele, 1956)	0.10	1.7
Wesslingsee, Bavaria, 10 M deep (Gessner, 1949)	0.9	....
Pool, 30 cm. deep (Gessner, 1949)	1.3	....
Lake Suwa, Japan, M deep (Ichimura, 1954)		
Summer	0.2	1.4
Winter	0.006	6.3
Wisconsin Lakes, M deep (Manning and Juday, 1941)	0.05–1.0	0.8–3.6
Dinoflagellate bloom, New Haven Conn. marine (Conover, 1954)	0.10	1.7
Lunzer Untersee (Gessner, 1949)	0.60	....
Lake Washington, Washington (Edmondson, Anderson and Peterson, 1956)	0.015–0.075	5
Diatom bloom, Moriches bay, 1 M (Ryther et al., 1958)	0.20	4.5
Sewage Pond, Kadoka, S. D. (Bartsch and Allum, 1957) euphotic zone 20 cm.	1.5	2
Corpus Christi Bay, Texas, depth 4 m.		
August 9 and 22, 1957	0.036–0.200	....
Marine pool, stagnant, filled from flood tide,		
Port Aransas, Texas, Aug. 6, 1957, 1 m. deep	0.356	....
Gulf, Port Aransas, Texas, 30 M deep, January, 1958	0.18	....
REEF MATERIALS AND CALCAREOUS ALGAE		
Coral Reef, Eniwetok (Odum and Odum, 1955)		
Whole Reef	0.5	4.0
Anemone sheet, *Zoanthus pulchelus*, Lajas, Puerto Rico	0.92	....
Reef corals and calcareous algae, Lajas, Puerto Rico		
Montastrea sp.	0.31	....
Porites asteroides	1.54	....
Dendrogyra cylindricus	1.35	....
Diploria clivosa	0.98	....
Penicillus capitatus ball, from center	1.72	....
Halimeda opuntia clump	2.75	....
ALGAL CULTURES		
Chlorella film, dense (Myers, 1954)		
Chlorophyll estimated from biomass	0.5	3.0
Sewage culture (Ludwig, et al, 1951)	....	2.0
Dunaliella culture (Ryther 1956a)	....	1–6
LITTORAL AND EMERGENT PLANT COMMUNITIES		
Water Hyacinth, Guadalupe River, Route 35, Texas,		
Eichornia, June 23, 1958	1.38(1.20, 1.72)	....
Attached Algae on the Jetty at Port Aransas, Texas,		
Gelidium sp., Ulva fasciola, and *Cladophora fasciculus*	0.66–0.91	....
Centroceras clavulatum	0.09–0.24	....
Encrustations	0.72	....
Spartina sp., Port Aransas, Texas, March 4, 1958	0.105–0.27	....
Algal scum on intertidal mud, Port Aransas, Texas	0.215	....
Salicornia sp., Laguna Madre, Texas, August, 1957	0.054–0.20	....
Rocky shore intertidal seaweeds Woods Hole, Mass.		
(E. P. Odum and Gifford, personal communication)	0.5–1.5	....
Red Mangrove Swamp, *Rhizopora*, Lajas, Puerto Rico	0.38	0.42
Black Mangrove Swamp, *Avicennia*, Lajas, Puerto Rico	0.48	0.45
Sand in the surf zone, Port Aransas, Texas	0.00	....
Cattail Marsh, July 22, 1957, Aransas Pass, Texas	0.94	....

TABLE 2—Continued

Chlorophyll and Assimilation Number in Communities

	Euphotic Zone Chlorophyll "A" Gm./M.^{2}	Assimilation[a] Number Oxygen gm./gm./hr.
SHALLOW AQUATIC COMMUNITIES WITH BOTTOM PLANTS (plankton minor)		
Silver Springs, freshwater eelgrass, *Sagittaria*, 1.7 M deep	3.0	0.5
Turtle Grass, Lajas, Puerto Rico, *Thalassia*, 1 M deep	0.43	....
Laguna Madre, Texas, Diplanthera, 1 M deep	0.041–0.30	0.5–1.5
Redfish Bay, Port Aransas, Texas, benthic plants 0.5 M deep:		
Winter		
Thalassia	0.06–0.48	....
Diplanthera	0.08–0.15	....
Lorentia	0.007	....
Upper ooze algae	0.09–0.23	....
Encrusted wood	0.067	....
Summer Mean of 3, July 7–8, 1957	1.0	2.0
Blue green algal mat, 0.1 M deep, salt flats of Laguna Madre, Texas, January, 1957	0.28–0.38	....
Blue green algal mat, 2 cm. deep, artesian water trough, Beaufort, N. C., August, 1956	0.66	....
Blue green algal mat, temporary salt pond, Portland, Texas, 0.1 M deep, May 26, 1958	0.55 (0.38–0.75)	0.02
Minter Spring, Brazos Co., Texas, pH 5.8 algae on brick walls (Abbott and Hoese)	0.45	....
Algal ooze on sand, Laguna Madre, Texas, January,	0.32–0.60	....
Rocky mountain stream, Utah, McConnell (1958)	0.3–1.6	0.7–2.0
Algae on live oyster reef, 1 M deep, turbid, Galveston Bay, Texas	0.32–0.41	....
Blue-green algal mat in flowing microcosm (Odum and Hoskin, 1957)	0.03–0.38	0.7–2.1
Aufwuchs on glass slides, Silver Springs (Yount, 1956)	0.5–1.5	....
Blue-green algal mat, polluted stream, Mission River, Refugio, Texas, Aug. 9, 1957	2.5	....
TERRESTRIAL COMMUNITIES		
Northern Europe		
Beech Forest (Gessner, 1949)	1.3	....
Birch Forest (Gessner, 1949)	0.9	....
Meadow, *Dactylis glomerata, Galium molugo* (Gessner, 1949)	1.0	....
Lower Montane Rainforest, Puerto Rico (Odum, Abbott, and Selander, unpublished data)	3.0	4
Domestic Red Clover, Port Aransas, Texas, March 5, 1958	0.59–0.81	....
Sugar Cane, Mature, Lajas, Puerto Rico, January, 1958 (Net)	2.5	0.5
Dune Grass, Port Aransas, Texas, July, 1957	0.1–0.8	....
Live Oak, Aransas Pass, Texas, July, 1957	0.51–1.68	....
Opuntia sp., after rains, Aransas Pass, Texas, July, 1957, computed per area of cactus patch	4.0	....
Opuntia dilleni, Lajas, Puerto Rico, dry season, computed per area of cactus patch	0.78	....
Mesquite thicket, Aransas Pass, Texas, July, 1957	0.74–1.1	....
Desert herbs, Agua Dulce, Texas, August 1, 1957	0.16–0.085	....
Old field, mixed plants, July 22, 1957, Aransas Pass, Texas	0.032	....
Pasture grasses, Welder Wildlife Refuge, Sinton, Texas, July 25, 1957	0.31–0.89	....

[a] New assimilation numbers of land communities reported here were made with a modified CO_2 absorption train adapted by W. Abbott from a system in use by Dr. L. Pomeroy of the University of Georgia Marine Institute. Measurements of community metabolism of aquatic communities are measured with diurnal curves, bottle methods and bell jars (Odum and Hoskins, 1958; and Park, Hood, and Odum, 1958).

TABLE 3

Comparison of Chlorophyll and Assimilation Number in Benthic Plants and Phytoplankton in the Laguna Madre of Texas

	Chlorophyll "A" Gm./M.^{2}	Assimilation Number Oxygen gm./gm./hr.
WINTER, 1957		
Plankton	0.002–0.043	2.7–4.5[b]
Benthos:		
Diplanthera wrightii	0.012–0.019	....
Bottom ooze, upper 1 cm.	0.029–0.071	
Total Benthos	0.041–0.090	0.75–1.5[c]
SUMMER, 1957 (August)		
Plankton	0.031	....
Benthos:		
Diplanthera wrightii	0.08–0.28	....
Bottom ooze, upper 1 cm.	0.094	
Total Benthos	0.27	1.5[a]
FALL, 1957		
Benthos:		
Diplanthera wrightii	0.018–0.16	....
Bottom ooze, upper 1 cm.	0.010–0.013	....
Total Benthos	0.090–0.17	. .
SPRING, 1958		
Plankton	0.002	3.8[b]
Benthos:		
Diplanthera wrightii	0.041–0.180	....
Bottom ooze, upper 1 cm.	0.106–0.120	
Total Benthos	0.15–0.30	0.5–0.9[c]

[a] Diurnal curve method.
[b] Light and dark bottle method.
[c] Light and dark bell jars.

in their systems of chlorophyll control means for keeping the chlorophyll at a low concentration until the time at which it normally becomes effective.

It is also possible that some plants are adapted to exist indefinitely with a mixture of heterotrophic and photosynthetic energy sources. Myers and Graham (1956) suggest such plants may develop less chlorophyll for the same light intensity than if photosynthesis were the only energy source. Some such explanation may account for the low concentrations of chlorophyll per leaf or cell in bromeliads in the rain forest (unpublished data), *Ochromonas* studied by Myers and Graham (1956), some shade leaves on the lower parts of trees, some herbaceous ferns, and some plankton.

In communities it is possible that chlorophyll of heterotrophs may serve as a concealing agent or a means to shade out competitors. For example leaves may be maintained on trees even below compensation point thus removing light that might be used by efficient ground competitors for soil nutrients.

Chlorophyll in Communities

As described in the preceding review and theoretical section, the chlorophyll of whole communities is a function of the several mechanisms and environmental factors. The interplay of the various factors produces varied patterns in vertical chlorophyll structure, in temporal sequence, and in the extremely diverse situations where life exists. In the following paragraphs brief mention is made of some patterns that result when environmental factors affect the chlorophyll adaptation mechanisms in nature.

Comparative Chlorophyll Data from Diverse Communities

In Table 2 are gathered Chlorophyll "A" data for the whole euphotic zone of various kinds of communities. Although more divergent than Gessner's first report (1949) indicated, the data are similar in order of magnitude. In seasons with maximum light intensity the Chlorophyll "A" ranges from about 0.1 gm./M^2 to 3.0 gm./M^2. Lower values are found in seasons with less light and in environments limited by extreme environmental factors.

The general green appearance of terrestrial communities is reflected in high Chlorophyll "A" values. Where clear waters are present so that high light intensities can reach aquatic plants, chlorophyll values in the water may approach those on land. For example, reef substrates, shallow and fertile algal blooms, Silver Springs, and aufwuchs may develop 1 to 3 gm./M^2 Chlorophyll "A".

Correlations of Chlorophyll "A" with conditions favoring photosynthetic fertility have been confirmed. Low values, for example, have been found in plankton of the sea beach, a cactus patch in a dry regime, winter conditions where cloud covers are heavy, and in bays turbid and shaded by silt. High values were found for such generally productive types as water hyacinths, cattails, intertidal algae on rock jetties, fertilized and shallow stream bottoms, and rain forests.

The general relationship of community chlorophyll and photosynthesis is indicated by the general uniformity of assimilation numbers which range generally 0.4 to 4.0 gm./gm./hr. (Table 2). These community assimilation numbers may be expected to be more conservative than the assimilation numbers of community parts. Whereas the assimilation number of cells varies with age, light adaptation, and nutrients, a community tends to have some of all kinds of physiological states with a less extreme mean.

From the range of data in Table 2 it is concluded that no one assimilation number may be assumed for all communities at every season, but it may be possible to predict assimilation values for a type of community if something of the conditions of light, age, and nutrient abundance is known.

In general plankton communities have somewhat larger assimilation numbers than leafy and thick celled systems. In Laguna Madre (Table 3) where plankton simultaneously share productivity with bottom plants, assimilation numbers for plankton (2 to 4.5 gm./gm./hr.) are higher than the values in the benthos (0.5–1.5 gm./gm./hr.). For terrestrial communities data on assimilation numbers are too few for generalization, although there are as yet no reasons to expect differences.

Vertical Distribution of Chlorophyll in Communities

Several of the factors discussed in the theoretical sections of the paper affect the vertical structure of chlorophyll in the natural community in known ways. Light decreases from the surface downward producing more chlorophyll and lower assimilation numbers with depth. In nature, however, factors other than light are also important. The presence of better nutrient conditions from regeneration at the bottom of a water body tends to increase assimilation numbers there. The stratification of aquatic herbivores in the shade during the day tends to decrease chlorophyll at the bottom by herbivore grazing. For example, Anderson (1958) showed the role of grazing in limiting chlorophyll in experimental lake studies. In some eutrophic lakes with shallow clear epilimnions the euphotic zone may be in the hypolimnion with favorable conditions for

accumulation of sinking, non-functional chlorophyll. The oxygen content of the hypolimnion thus can affect the chlorophyll by limiting the herbivore populations. In stratified situations, high temperature at the top may increase assimilation numbers there. The turbulence may control the size of plant cells that may be suspended, Riley, Stommel, and Bumpus (1949). With more turbulence, larger cells are possible with more chlorophyll per community area, less chlorophyll per gram, and lower assimilation numbers. Vertical layering of species is well known. See Talling (1957) for a recent example and discussion of the stratification of phytoplankton populations. Unless there are motile or floating species, cells fall away from the very topmost surface even in very turbulent conditions.

Whereas the top of a stratified community adapted to high light intensity may have high assimilation numbers (Ichimura, 1956) and less chlorophyll per cell, other communities like those in the mixing epilimnetic waters of lakes and seas may have cells adapted to an average position in their daily rises and falls. Uniform concentrations of chlorophyll with depth often occur especially during times of vertical mixing (Manning and Juday, 1941; Ichimura and Siajo, 1958). Such cells may not be genetically capable of adaptation to the highest steady light intensity to the extent of species adapted remain at the top of stratified communities.

Dinoflagellates and other species are known to move vertically concentrating sometimes at the surface and sometimes at deeper levels. In shallow pools some algae may coat the surface with such density that the euphotic zone is only centimeters thick. Pomeroy, Hakin and Ragotzkie (1956) found much of chlorophyll in topmost layers in some dinoflagellate blooms. Bartsch and Allum (1957) found decreasing chlorophyll with depth in stratified sewage pond with a euphotic zone of 20 cm.

All of the varying factors may tend to produce many different patterns of vertical chlorophyll structure. Kozminski (1938) reported 4 types of vertical patterns in Wisconsin lakes. Riley (1940) found all four types in Linsley pond at different times, and Jenkins (1955) found all types in the English channel at different times. Hogetsu and Ichimura (1954) described lakes with chlorophyll increasing with depth in lakes whereas Kozminski (1938) and Manning and Juday (1941) found many waters with chlorophyll increasing with depth. The relative roles of light, grazing and other factors may be reflected in these differences.

The above authors describe many cases with maximum chlorophyll at an intermediate depth in the euphotic zone in lakes and seas especially, Riley, Stommel, and Bumpus (1949). A similar pattern exists in "grass" beds of Silver Springs (Odum, 1957). In a red mangrove swamp *(Rhizopora)* in La Parquerra, Lajas, Puerto Rico. the vertical distribution of Chlorophyll "A" in gm./M^2. of leaf contained a maximum at an intermediate level as follows:

above ground	gm./M^2
6M.	0.25
5M.	0.19
4M.	0.32
3M.	0.35
2M.	0.23
1M.	0.25

The reef structures in the windward reef at Eniwetok are within a meter of the surface in water of almost maximum clarity so that light penetration into the reef is likely to be maximal. As described previously (Odum and Odum, 1955), intense green bands of boring algae grow in all the substrates including the live corals. Elsewhere in Hawaii, Key West Florida, and La Parguerra, Puerto Rico, these authors have since had an opportunity to break open coral heads for comparison. Although some green bands exist, in general the intense banding observed in Eniwetok has not been observed. It seems likely that the greater depth and greater turbidity intercepts more of the incident light in the other areas examined. Thus less light penetrates into the limestone to support deep-subsurface algal growth. The deep algal bands in reef materials are clearly in shade and are likely to have more chlorophyll per cell and a low assimilation number relative to the more brightly illuminated zooxanthellae which are in a zone of light adaptation.

With so many kinds of vertical chlorophyll patterns it is not possible to assume vertical chlorophyll structure or to consider as representative chlorophyll measurements per volume from only part of the euphotic column. It remains for further work to determine if the various vertical chlorophyll patterns are in each case self adapted for maximum community photosynthesis under the circumstances as postulated in the previous sections.

Seasonal Changes of Chlorophyll in Communities

The chlorophyll in the euphotic zone of a community in the course of a year is subject to changes in many of the aforementioned controlling factors, nutrients, temperature, turbulence, and grazing by herbivores. Thus with different annual factor sequences in different areas, annual patterns of chlorophyll differ also. The chlorophyll of the whole euphotic zone increases with light, with nutrients, when graizng diminishes. and with conditions leading to retarded chemical turnover in the cells. The area-based assimilation number for the whole euphotic zone increases with light, nutrients, temperature. and conditions favoring high turnover rates.

Many annual curves for chlorophyll and assimilation number have been reported; there is no generalized pattern. Riley, Stommel, and Bumpus (1949), Atkins and Jenkins (1953), and Conover (1954), for example, frequently found maximum chlorophyll and assimilation number in the spring since conditions of increasing light, low grazing. and maximal nutrients often occurred together. Gessner (1944) found low assimilation numbers in winter. Further south Margalef, Munoz and Herrera (1957) found more plant pigments on the Spanish coast in winter. In 3 Japanese lakes Hogetsu and Ichimura (1954) and Ichimura (1956) found that maximum chlorophyll of the whole euphotic zone was in the summer. Much non-functional chlorophyll was found sinking into the dark hypolimnion. Anderson (1958) found high chlorophyll values in spring and early fall in saline Lake Lenore, but in Soap Lake chlorophyll was minimal in Fall. In the present study seasonal comparisons in the Laguna Madre of Texas (Table 3) indicate lower chlorophyll contents, lower production, and higher assimilation numbers in the winter season. N. Marshall (1955) found as much variation in Alligator Harbor, Florida from day to day as seasonally. In these varied sequences there is neither proof nor disproof for theories of chlorophyll adaptability but increasing knowledge of seasonal patterns advances the science of comparative ecology and may permit more

accurate use of chlorophyll and assimilation number for measurement of primary photosynthesis.

Chlorophyll, Community Age, and Succession

Although a number of authors have studied the time sequence of chlorophyll and photosynthesis of single plants and algal cultures as age studies, it is difficult to separate the effects of physiological age from such community properties as diminishing nutrients and self-shading.

If with old age a machine decreases the effectiveness of its energy transfers with more energy lost to leakages, more input energy may be required for the same work output. In the cannon-ball catcher machine analogy more cups may be needed as the machine ages in order to accomplish the same job. Whether the increase of chlorophyll with age of cells has any similarity of basis with senescence of the cannonball catcher is unknown.

The increase in chlorophyll in an aging culture or plant is related to the increased self shading. Cells from older plants and cultures are larger with less turnover, more chlorophyll, and lower assimilation numbers (Willstatter and Stoll, 1918; Ludwig, Ostwald, Gotaas, and Lynch, 1951). Margalef (1957) found more chlorophyll, larger size, and lower turnover in older cells of *Scenedesmus obliquus*. Self respiration rate is higher so that self nutrient regeneration is greater. Thus several factors affect chlorophyll simultaneously in an aging plant or culture. Individual Chlorella cells growing in synchronous culture developed maximum photosynthesis 3–4 hours after division (Sorokin, 1957). Whether a community has age other than the age of its individuals has yet to be determined. At present community time sequences are termed succession.

In plant succession in nature, early colonization is followed first by increases in community chlorophyll, bright conditions, and high assimilation numbers. Later these may decline. There is no certainty whether the last and most stable stages of succession have as much chlorophyll and assimilation as intermediate stages. A flowing microcosm (Odum and Hoskin, 1957) had maximum chlorophyll and assimilation during favorable nutrient conditions of succession. The spring blooms in north temperature waters are accompanied by excessive chlorophyll and assimilation followed by later stages with lower values. Very high chlorophyll contents have also been found in climax rainforests and coral reefs.

Thus as yet there is no proved single sequence of chlorophyll and assimilation number in succession. It is likely that communities can be grouped according to productivity sequences for predictive purposes.

Diurnal Changes in Chlorophyll

It may be postulated that the adaptive mechanisms suggested above as the cause of the temporal variation in chlorophyll also operate in daily cycles. Diurnal variations in exported chlorophyll with midday maximum were measured in Silver Springs (Odum, 1957). Diurnal variation of plankton chlorophyll has been shown in several environments. Mr. Ray S. Wheeler (unpublished student report, Duke University, 1956) in an estuarine lagoon near Beaufort, N. C. found a diurnal range 6 to 25 mg. chlorophyll per M^3 with maximum amounts in the afternoon. Yentsch and Ryther (1957) and Shimada (1958) found a maximum chlorophyll per volume of water at dawn in marine waters although the daily variation in chlorophyll of the total euphotic column was not

measured. Ten measurements in Copano Bay, near Port Aransas, Texas showed a wide range (0–25 mg./M^3) Mitrakos, Bünning, and Ebshadt (1957) found a 10 per cent diurnal variation in chlorophyll content of leaves of a land plant, *Perilla ocymoides* with more chlorophyll in the middle of the day.

A diurnal variation in assimilation number was found in Lake Teganuma by Ichimura (1958) with a noon maximum.

It is not difficult hypothetically to interpret the diurnal maxima in terms of adjustments of chlorophyll to maintain optimum output drive. For example, early morning chlorophyll maxima in a cell may be attributed to the need for more chlorophyll per cell at low light intensity. Nutrient depletion and temperature rise late in the day may prevent the rise of the chlorophyll in the evening.

Area-Based Procedure for Determining Community Photosynthesis From Chlorophyll

There have been a number of attempts to measure photosynthetic rate from chlorophyll measurements as a field method in aquatic ecology (Riley, 1940; Manning and Juday, 1941; Edmondsen and Edmondsen, 1947; Hogetsu and Ichimura, 1954; Edmondsen, 1955; Ryther, 1956b; Ryther and Yentsch, 1957, 1958; Holmes, Shaefer, and Shimada, 1957 and others). These studies have dealt with plankton communities and have been based on chlorophyll concentrations per volume. For example, Ryther and Yentsch in work in the North Atlantic and coastal waters of the northeastern United States measure the chlorophyll concentration, the extinction coefficient of light in the euphotic zone, an assumed assimilation number based on previous photosynthetic measurements in similar environments, and an assumed vertical distribution of assimilation numbers. As indicated by data in Table 2, such methods are not general since assimilation number varies. Even in plankton communities there is no reason to expect assimilation numbers to be constant. Holmes, Shaefer, and Shimada (1957) were unable to confirm the chlorophyll procedure as used by Ryther and Yentsch for other areas. Such methods which involve knowledge or assumptions of structure are not readily adapted to diverse communities on land, reefs, and shallow bays where the euphotic zone may be variable or concentrated in a thin layer.

In order to make the chlorophyll method more general it is suggested that chlorophyll and assimilation numbers be measured for the whole euphotic zone per area as in Table 2. For each type of community measurements should be made at all seasons, light, and nutrient regimes, so that a group of assimilation numbers become available. Thereafter, it will be possible for photosynthesis to be related to chlorophyll with more certainty.

For example, data summarized in Table 3 for the upper Laguna Madre of Texas can be used there in subsequent years with occasional checks to provide rapid estimates of the primary production from the relatively rapid survey of chlorophyll. The chlorophyll methods previously used by aquatic ecologists can thus be adapted for community work on land as suggested by the preliminary measurements in this paper. Even where no measurements of assimilation number are made, it may be possible to develop approximate data on community photosynthesis of land areas by use of assimilation numbers of somewhat similar community systems. The role of important land factors such as water in controlling production in arid areas may be followed with community chlorophyll assay.

Under natural conditions the period of insolation from which the assimilation number is computed should be considered. Ideally the period of measurement should be an entire day and the results presented as grams of oxygen per gram of chlorophyll per *average* hour of insolation. An exact half of a solar day seems to be the next most favorable period although there is no evidence to indicate that symmetry of photosynthetic activity may be assumed for half days.

Summary

1. Measurements of Chlorophyll "A" and assimilation number have been made in widely contrasting types of communities in order to permit generalization about distribution and role of chlorophyll in ecology on land as well as in water. The chlorophyll of whole euphotic zones in well lighted seasons generally ranges from 0.1 to 3.0 gm./M^2. The assimilation number of such whole communities generally ranges from 0.4 to 4.0 gm. 0_2/gm. Chlorophyll "A"/hr.

2. The cannon-ball catcher analogy is utilized to explain some known adjustments of chlorophyll. Chlorophyll "A" systems are believed self adjustable for maintaining optimum input-output power ratios. Changing the numbers of cups of the cannon-ball catcher machine is energetically equivalent to changing the amount of chlorophyll. The role of the ecological community in controlling the system of chlorophyll in nature is postulated. The difference between adaptation of single plants and the adaptation of the whole community is emphasized.

3. Measurments with both the Beckman DU spectrophotometer and the Bausch and Lomb spectrophotometer have been made in order to adapt the chlorophyll method of Richards and Thompson (1952) to general ecological use. The abbreviated equation for chlorophyll when extracted with 90 per cent acetone and measured with a narrow band pass spectrophotometer is: Chlorophyll "A" in mg./l = 13.4 (optical density at 665 millimicrons with 1 cm. light path). Measurements with a broad band pass instrument require slightly different conversion factors depending on the types of plants.

4. Measurements are reported indicating the impracticality of separating functional and non-functional chlorophyll. The convention of including all euphotic zone chlorophyll is suggested.

5. Errors in chlorophyll assay due to extraction procedures, solvent variation, and assumptions in the Richards and Thompson procedure are discussed. Errors are in general less than those due to sampling error and the great variability of natural chlorophyll distribution.

6. Communities are classified in four types with respect to light intensity-chlorophyll adjustments: (1) stratified communities with levels of light-shade adaptation. (2) shaded communities. (3) mixing communities with plant cells exposed to fluctuating light intensity. (4) bright thin communities without shade adapted parts. Total chlorophyll and total community photosynthesis is maximal in stratified type (1–60 gm./M^2/day). Assimilation number is maximal in the thin bright type (8 to 40 gm. oxygen/gm. Chlorophyll "A"/hour). Efficiency is greatest in the shaded community type (10 to 30%).

7. Total photosynthesis and chlorophyll of whole euphotic zones (unlike the photosynthesis and chlorophyll of community parts) increases with light intensity without a maximum even at full sunlight. These are exceptions.

8. Cannon-ball catcher theory is presented to account for the low concentrations of community chlorophyll with limiting nutrients, with high temperatures, with small plant size, with heterotrophy, and in water as contrasted with land.

9. Data on the annual and vertical patterns of chlorophyll are reviewed in terms of the factors controlling community chlorophyll adaptation. There are no universal patterns for maxima and minima, but characteristic types exist for particular kinds of communities.

10. For greatest comparative value and least variability, measurements of chlorophyll for the purpose of estimating photosynthesis should be made for the whole euphotic zone on an area of community basis. Photosynthetic measurement procedures based on single assimilation numbers do not have general applicability. For maximum accuracy community assimilation numbers must be determined for each characteristic environment, condition, and season.

Rough community photosynthesis values may be obtained in unknown communities by selection of assimilation numbers reported for similar community types from data like that in Table 2. With adequate caution the abbreviated chlorophyll method may be used widely over the communities of the earth to obtain production estimates where direct measurements are prohibitive in cost.

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Seasonal Growth of Benthic Marine Plants as Related to Environmental Factors in an Estuary[1]

JOHN T. CONOVER

Institute of Marine Science
The University of Texas
Port Aransas, Texas

Abstract

A study was made of the standing crops of 70 taxa of benthic marine plants and some physical, chemical, and biotic agents in a tidal estuary. Seasonal comparisons were made between plant growth and environmental factors from 1952 to 1954.

The standing crop of benthic marine plants was in excess of 4.0 kg. wet weight per square meter during July and August and less than 1.5 kg. in January. Temperature and illumination were variously associated with the maximum seasonal growth of those benthic plants studied. Some species, including *Cladophora gracilis* F. *tenuis*, *Enteromorpha linza*, E. *plumosa*, *Stilophora rhizoides*, and *Ulva lactuca* var. *latissima*, grew best under conditions of high insolation (over 500 gram calories per square centimeter per day) at moderate water temperatures (18° to 20° C.). Others, including *Agardhiella tenera*, *Enteromorpha compressa*, *Gracilaria verrucosa*, *Ruppa maritima* and *Zostera marina*, showed increased growth under diminished light intensities (less than 400 gram calories per square centimeter per day) at high water temperatures (over 24° C.). The low calculated seasonal yield of one group, including *Enteromorpha clathrata*, *E. intestinalis*, *Ectocarpus siliculosus*, *Gracilaria verrucosa*, *Polysiphonia novae-angliae*, *Punctaria plantaginea*, and *Scytosiphon lomentaria* was related to low concentrations of inorganic phosphate (less than 0.4 microgram atoms/liter P) in the spring (April and May) and nitrate (less than 0.2 microgram atoms/liter N) in the fall (October).

Forty-seven of the 70 taxa flourished in the tidal and brackish areas of the estuary. Sixteen of the 70, including *Chondrus crispus*, *Corallina officinalis*, *Enteromorpha linza*, *Gelidium crinale*, *Nemalion multifidum*, *Petalonia fascia*, *Polysiphonia nigrescens*, *P. novae-angliae*, *Punctaria plantagineae*, *Sargassum filipendula* and *Ulva lactuca* var. *rigida* were found only in normal sea water at the mouth of the estuary. The occurrence of some species, including *Ceramium rubrum* var. *proliferum*, *Ectocarpus siliculosus*, *Gracilaria verrucosa*, *Spyridia filamentosa* and *Stilophora rhizoides*, in the brackish water sloughs in January and February and their absence in low salinity water in March and April, suggested some relationship with either rising temperatures or changes in water density.

Six species of *Vaucheria*, found only in the marshland between neap and spring high water levels, were observed to fruit in winter and early spring but attained best vegetative growth in mid-summer. Fruiting periods of all six species were associated with spring tides.

A large portion of the benthic plant populations of the major basin of the estuary was observed to receive large additions of algal sporelings which first became established on coarse beach sediments and after some growth were wave-transported onto the silt-laden basin floor. These plants were still attached to small shells or pebbles. The effects of sedimentation, tidal currents, storm and hurricane winds, ice, and freezing are described. The aperiodic occurrences of some species in the area from 1952 through 1956 remain unexplained.

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Introduction

The present investigation concerns seasonal periodicity in the growth and reproduction of larger aquatic plants in an estuary. In an early paper F. E. Fritsch (1906) stated that the seasonal phenomena eventually would be explored on a quantitative basis by estimating phytoproductivity, by measuring the important environmental features, and then by comparing these data in search of causal relationships. Fritsch's suggested program of study was proffered at a time when the science of ecology was quite new. Development of the proper methods was to take a number of decades. With remarkable early insight he perceived two kinds of seasonal change: regular periodic changes and irregular ones. Regular patterns he described as those recurring normally each year in seasonal sequence, while irregular changes had no fixed pattern of occurrence and could take place at any season.

Fritsch suggested that there were probably both direct and indirect forces in the en-

vironment which had an impact on periodicity in plants. Light and temperature he believed to be direct, while all others were indirect as part of a complex affecting the organism. This point of view has not changed essentially over the intervening 50 years.

The present study was undertaken to determine the relative importance of several environmental agents affecting events in the seasonal histories of the dominant, benthic, multicellular marine plants in a specialized marine habitat. The investigation was confined to a representative, relatively self-contained estuary, Great Pond, near Woods Hole on the southern shores of Cape Cod, Massachusetts (Fig. 1).

Review of Related Work

Over the past 50 years most studies of the seasonal occurrence and growth of benthic marine plants have been descriptive. Excellent summaries of these descriptive studies are given by Funk (1927), J. Feldmann (1937, 1951), Fritsch (1945) and Bernatowicz (1952a). More recently a number of limited, quantitative studies have increased our knowledge of seasonal growth. Yet, as Blinks (1955) has pointed out, "Long term (seasonal or yearly) production of organic matter has not been studied as thoroughly in littoral algae as in algae of the open ocean."

Qualitative studies indicate that some plants grow throughout the year while others have dormant periods (Kylin, 1907). In Ceylon at approximately 8° N. Lat. maximum plant cover is believed to occur in spring followed by a decrease in summer with the minimum appearing in autumn (Svedelius, 1906). Some algal species in Swedish coastal waters show greatest vegetative growth in late winter and early spring (Printz, 1939). Rees (1934, 1935) found the peak vegetation cover for the coast of Wales to occur in mid-summer. Certain species, for example *Fucus vesiculosus* and *Ectocarpus siliculosus,* may show best growth in summer in polar seas but seem to exhibit maximum cover in winter in warm temperate waters (Knight and Parke, 1931). The benthic vegetation of Bermuda at 32° N. Lat. may be similar in its seasonal growth cycle to that reported for Ceylon (Bernatowicz, 1952a). Since all these studies are based upon visual estimates, the conclusions are questionable. These results can be confirmed only by using quantitative ecological techniques.

A few quantitative studies using such techniques have been made over the past 40 years. Early studies include those of Petersen (1912) and Boysen-Jensen (1941), who attempted standing crop estimates for *Zostera marina.* More recently, improved methods have shown that high growth rates generally occur during the spring in temperate waters. Dry weight increases in *Laminaria* (Black, 1950) and in *Ascophyllum nodosum* (Printz, 1950) indicate maximum growth for these species in the spring. Knight and Parke (1950) reported growth rates of 0.5 to 0.85 cm./week for *Fucus serratus* and *F. vesiculosus.* Estimates for *Macrocystis pyrifera* showed yields of several kg./M^2/yr. in the extensive kelp beds of California (Sargent and Lantrip, 1952). Annual yields up to 10 g./M^2/yr. have been reported for kelp in the coastal beds of Scottish waters (Inst. Sea Weed Res., 1953). Carpelan (in Blinks, 1955) gave spring and fall growth estimates in temperate seas ranging from 70 g./M^2/yr. dry weight for *Ulva* to 4.4 kg./M^2/yr. for blades of *Laminaria.* Blinks (1955) compared these values with the 0.5 g./M^2/yr. reported for phytoplankton. The red alga, *Iridophycus cornicopeae,* in a locality in Japanese waters, attained a maximum standing crop in the spring (Hasegawa and Fukuhara, 1956). Several workers have shown early spring growth maxima for *Porphyra.* Although these studies represent a commendable beginning, most have not included com-

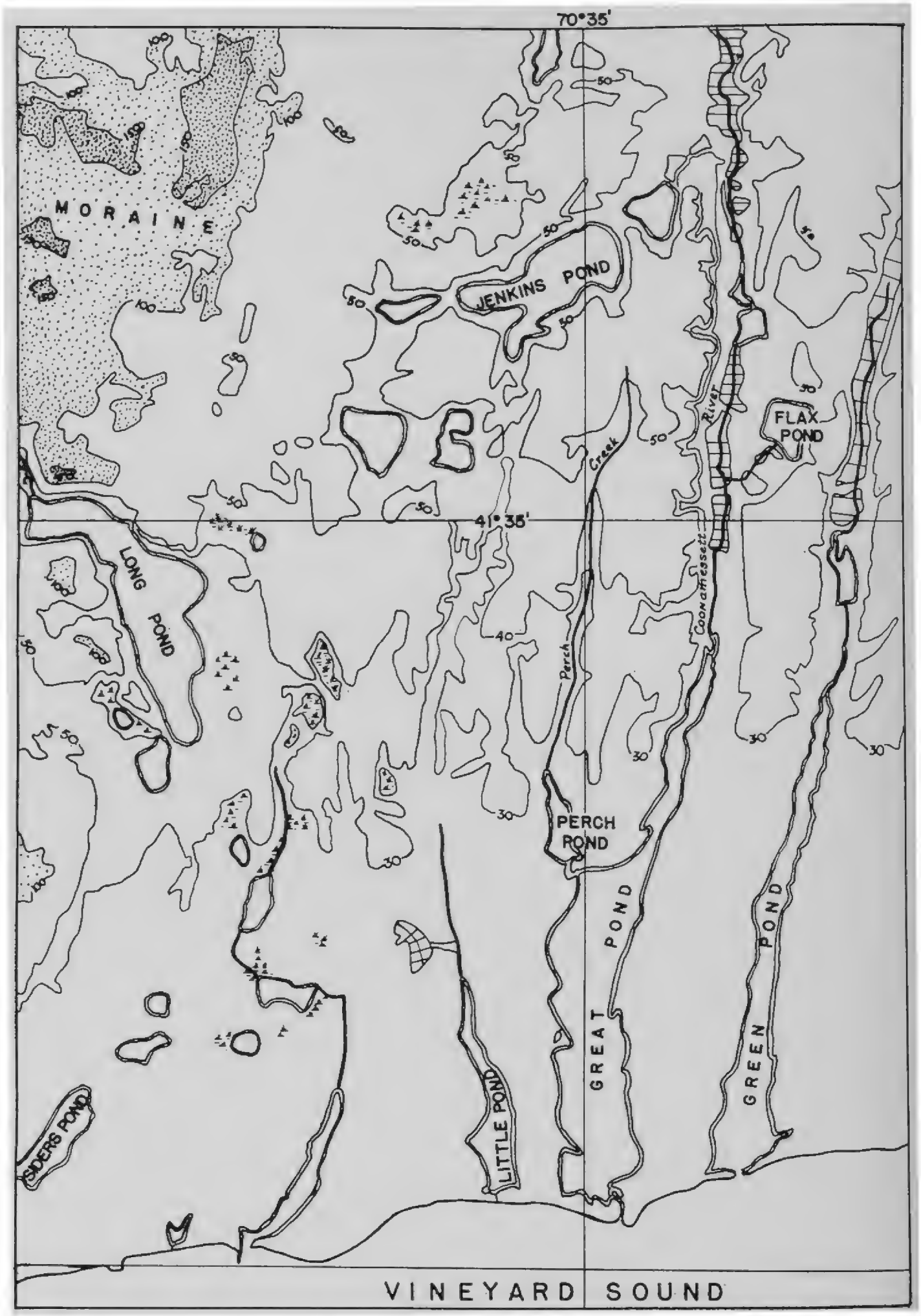

FIG. 1. Map of Great Pond, Falmouth, Mass. after a U. S. Geological Survey Map showing the drainage basin and the Wisconsin Moraine. The rectilinear areas are cranberry bogs. Contour intervals are in feet. Only 30, 50, and 100 foot contours are drawn. One inch approximately equals one mile.

plete seasonal cycles of growth. Moreover, none of these studies have measured entire benthic plant communities.

The relationship between light and the seasonal growth of benthic marine plants is

little understood even today. Reviews of work concerned with the subject appear in papers by Fogg (1953), Blinks (1955) and Holmes (1957). A review of important contributions which apply to the present study follows. Svedelius (1906) believed light was the major factor affecting growth at low latitudes. No investigator has confirmed these observations with quantitative ecological methods. In temperate seas growth optima were demonstrated for plants of low and high light intensity types in both fresh and salt water (Ehrke, 1929, 1931). Some kelps have been shown to attain higher standing crops at depth betwen 4 and 8 meters presumably due to the efficiency of the auxiliary pigments in green light. Walker (1952) found a reduction in the density of kelps at depths below 2 meters, perhaps related to the diminishing quality and intensity of light. In *Macrocystis pyrifera* the synthesis of sugars takes place mostly in the assimilatory tissues of the fronds at or near the surface (Sargent and Lantrip, 1952). Despite the evolution of special auxiliary pigments in red and brown algae, Blinks (1955) asserts that phytoproduction may always be highest at or near the surface in temperate seas. Some studies indicate that the uptake of carbon dioxide and hence the synthesis of organic matter by marine plants, may be limited by certain intensities of light (Holmes, 1957). Moreover, these so-called saturation values may vary from one species to another. Data cited by Holmes suggest that higher light intensities are required by a given plant for increases in photosynthesis than may be tolerated for maximum rates of cell division. These results suggest that various portions of the electromagnetic spectrum of energy from infra-red to ultra-violet may be affecting different phases of growth.

Temperature effects on growth concern still another aspect of radiant energy which governs biological processes. Gunter (1957), in his review of temperature and marine ecology, indicated the complexity of temperature studies. He stated, "Temperature is the most important single factor governing the occurrence and behavior of life. Temperature changes affect protoplasm directly and change the physical and biological environment as well." Attempts to correlate temperature with biological process have always been extremely difficult. Hedgpeth (1957) has given a summary of biological studies and principles including examples of benthic marine plant growth as related to temperature zonation. He considered temperature, with qualifications, as the most important single factor governing the distribution of life in the sea.

As early as 1851, W. H. Harvey considered temperature to be the major factor affecting plant growth and geographical distribution. Throughout its range from the Arctic to New Jersey, when water temperatures are between 3° and 6° C, *Ascophyllum nodosum* grows and produces oöspores (Setchell, 1920a, 1932). In arctic waters this temperature range occurs in midsummer but in southern New England and New Jersey these temperatures occur in midwinter. The behavior of this species is considered by Hedgpeth (1957) to be a good example in support of Hutchins' theory of temperature zonation. Setchell (1915, 1917, 1920a, 1920b) also developed an idea of temperature intervals and thermal zones. His concept was based upon 5° intervals of annual mean temperatures of a hemisphere along parallels of latitude, within which the broad distribution lines for benthic marine algae might be explained.

The study of growth rates has received some attention in more recent years. Klugh and Martin (1927) found the growth rates of some benthic algae decreased with depth and temperature. Laboratory experiments (Boyle and Doty, 1949) indicate that algal plants were killed more quickly at higher temperatures in dilute sea water than the control plants growing in normal sea water. Low killing temperatures for plants in brackish

water were about the same as those for the controls in normal sea water. There is a dearth of information, apparently, relating temperature to seasonal growth rates or standing crops. Many quantitative accounts mention temperature as probably affecting seasonal growth without supporting data for these assumptions.

The role of nutrients in seasonal growth of benthic marine plants has been singularly neglected. Among the few observations is a suggestion by Rochford (1952) that the interstitial phosphate in the muds of the more saline portions of shallow tidal estuaries may be readily available to shallow-bedded species of benthic algae, such as *Gracilaria.* He also considered the same phosphorus source as directly benefiting beds of the rooted immergent marine phanerogams such as *Zostera marina.* Although he found high concentrations of both phosphorus and nitrogen in the muds of estuaries in areas with good plant cover, no proof was offered that the plants did benefit from the mud reservoir of nutrients. There is much evidence from freshwater studies (Gessner, 1955) that rooted aquatic plants utilize nutrients from bottom muds.

Blinks (1955) has postulated that in the cycle of plant growth and decay in littoral communities along open coasts, the reserves of carbon, nitrogen and phosphorus, and other constituents of protoplasm, may be in such ever present excess as to be causally related to the very high phytoproductivity of coastal areas. A thorough study of the nutrient requirements and relationships between seasonal growth and the nutrient concentrations in nature awaits investigation.

A review (Doty and Newhouse, 1954) of several phases of the effects of salinity dilution by freshwater indicates no quantitative growth measurements have been made. Species of benthic marine plants which are present or absent along a diluted sea water gradient series have been listed in a number of studies by Luther (1951a, 1951b) and Doty and Newhouse (1954). Fassett (1928) described the zonation of immergent as well as emergent marine phanerogams as related to salinity in a marsh. Hoffmann (1929) reported that many marine plants tend to have higher respiration rates when growing in brackish water. Such plants may use up organic matter in respiration more rapidly than they can synthesize it due to low salinities. Sterility has often been reported in benthic plants growing in dilute sea water (Häyren, 1940, Levring, 1940; and others). Further studies are needed to separate with certainty those effects produced by differences in salinity from those effects which depend upon nutrients, light and temperature. We also need to know the physiological explanation for various growth and developmental responses to differences in salinity.

The pattern of algal periodicity in some areas is modified by the absence of suitable habitats for attachment at the time of sporulation. Some studies show that texture of the substratum (roughness, and hardness) is more important than chemical composition of the rock minerals (J. Feldmann, 1937, 1951). The presence or absence of lithophytes is profoundly affected by suitability of the bottom type (Rees, 1934; Levring, 1940; and others). Moul (personal communication) believes there is a "condition factor" brought about by previous plant and animal occupants preparing a substratum for attached plants sporulated in the following season.

In the survey of communities of Great Pond, those environmental factors measured were the same ones suggested as important to benthic plants from previous studies. These included light, temperature, salinity, nutrients and the character of the substrate.

Acknowledgements

I am most grateful for the guidance of Dr. Wm. Randolph Taylor, major professor during the course of this investigation and for the encouragement and suggestions of Dr. Alfred C. Redfield regarding the field problems. Thanks are given to Dr. Madeline Pierce for assistance in the field work, to Dr. Howard T. Odum for stimulation during the final writing, to Dr. John C. Ayers for suggestions regarding the nutrient cycles, to Drs. Kenneth L. Jones, Chester A. Arnold, Frederick K. Sparrow and Frederick E. Smith for advice as members of my Ph.D. committee, to Drs. Edward Moul and Maxwell Doty for counsel on the field problems and to Drs. Doty and Butcher for copies of unpublished manuscripts.

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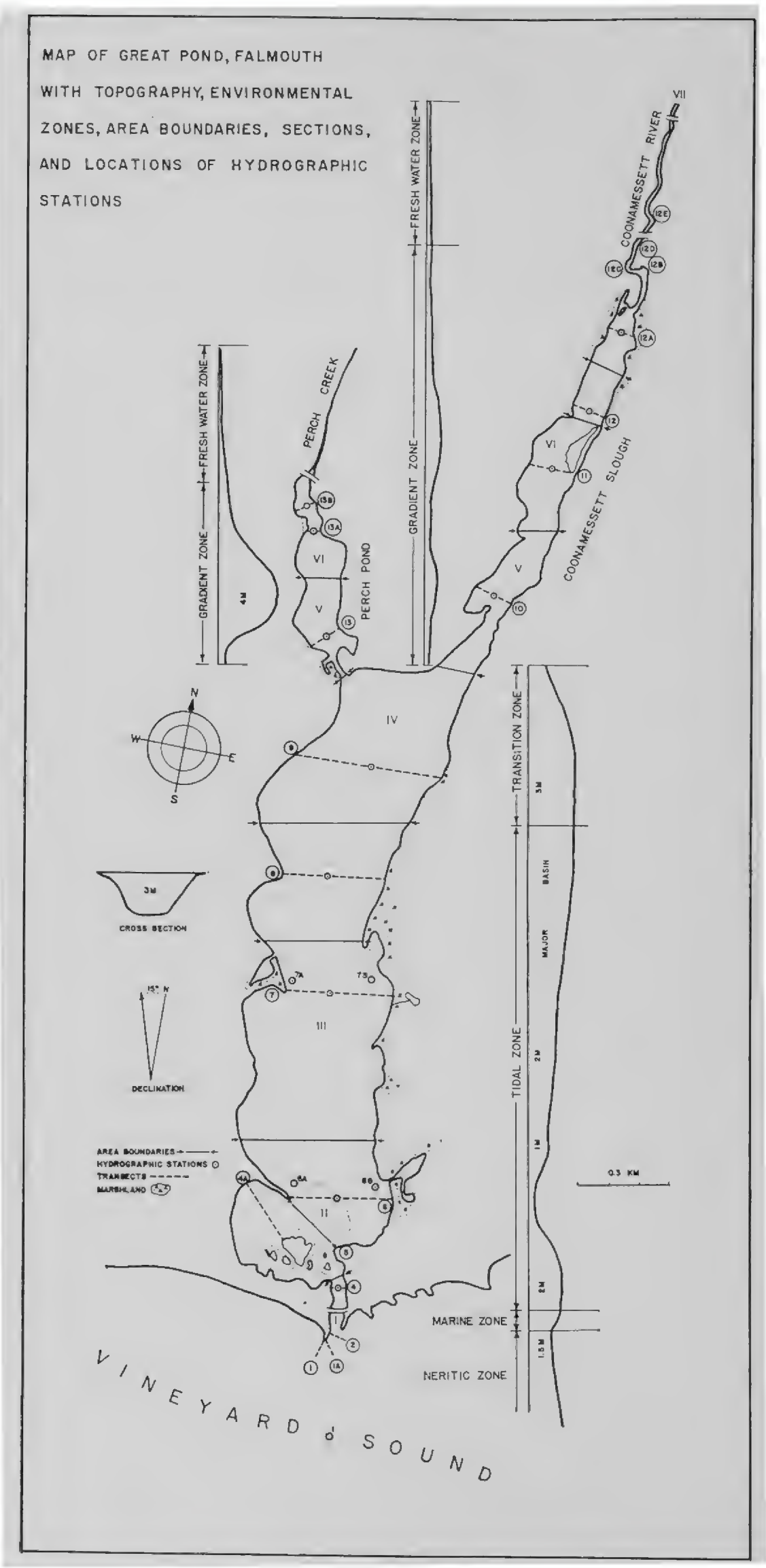
Methods

Sampling

Sixteen transects were established, generally orientated at right angles to the long axis of the estuary. Each transect represented an area and was designated by a section number. Time of sampling did not exceed 30 hours for one complete circuit of all stations. In addition, eight hours were scheduled for water analysis every two weeks.

Quadrats were established along each transect. In the intertidal zones on the rock jetty, 25 cm^2 quadrats were used (Fig. 2). Initially, paired transects were established about 30 meters apart to check reproducibility in the major basin. During the season of prevailing moderate southeast winds, when the test pairs were studied, fairly good agreement was obtained. However, after the upstream transect of each pair had been abandoned, there was some suspicion that waves reached the bottom during storm periods, changing their distribution and density, diminishing homogeneity. Deposition on the shore was common during severe northeast, southwest or tropical storms.

Fig. 2. Map of Great Pond, Falmouth, Mass., with topography, environmental zones, area boundaries, sections, and locations of hydrographic stations.


MAP OF GREAT POND, FALMOUTH
WITH TOPOGRAPHY, ENVIRONMENTAL
ZONES, AREA BOUNDARIES, SECTIONS,
AND LOCATIONS OF HYDROGRAPHIC
STATIONS
FRESH WATER ZONE
GRADIENT ZONE
4M
PERCH CREEK
PERCH POND
GRADIENT ZONE
FRESH WATER ZONE
COONAMESSETT RIVER
COONAMESSETT SLOUGH
VII
VI
V
IV
III
II
N
W
E
S
3M
CROSS SECTION
15° W
DECLINATION
AREA BOUNDARIES
HYDROGRAPHIC STATIONS
TRANSECTS
MARSH, AND
TRANSITION ZONE
5M
BASIN
MAJOR
2M
1M
TIDAL ZONE
0.3 KM
MARINE ZONE
NERITIC ZONE
1.5M
VINEYARD SOUND

Hydrographic stations were established in 1952–53 at the centers of all transects except 4A and 5 (Fig. 2). Station 1 was located 0.4 km. offshore in the sound and station 12E in the fresh water portion of the Coonamessett River above State Highway 28.

Measuring Plant Populations

Plant populations were counted on each quadrat. The cover was estimated and sampled with a specially designed scoop, 25 cm.^{2} in capture area covered with one cm.^{2} mesh wire. The scoop was attached to a four-meter pole. A hooded, glass-bottom scanning box was fastened to the side of the skiff. Samples of plants observed through the scanning box were taken with the scoop, identified, measured, preserved, labeled, and retained for further study. Fortunately, during the seasons when the sea water was too chilly for skin-diving, the turbidity was generally low, permitting good visibility of the bottom particularly on cloudy days. In the summer months, when turbidity was high, skin-diving proved effective.

Observations at all stations except on the jetty were made from a 9-foot skiff with outboard motor. A 25 cm.^{2} grid of dural tubing was improvised to mark off quadrats on the jetty. A meter-square grid guide, made from two one-meter brass rods, crossed at right angles and brazed together at their centers was lowered on a line to the bottom to mark off the meter-square under-water quadrats.

Estimates of percentage cover were made using the "percentage cover guide" method explained in detail in Braun-Blanquet (1932). This method makes use of guides for three types of area cover: checkered, solid block, and asymetrical body figure grids. The percentage cover guide is first used to train the investigator's accuracy in estimating plant cover and later serves as a reminder. The writer made trial runs which proved to be reproducible within a 5 percent significance level at the low end of the scale and 10 percent at the upper end. Since detailed data also were recorded regarding thickness of an algal mat, estimates of area and volume of many populations could be computed from the measurements.

Cover estimates were first obtained in the field from an average of three grid counts per quadrat. These data were totaled for all quadrats on each transect.

An aerial photograph, taken by a U. S. Navy airplane on December 10, 1954, showed the presence of scattered patches of material on the bottom which were believed to be large clumps of algae. The patterns seen from above resembled the patterns developed in the cover surveys.

For each species average percentage cover for each section was obtained from the average for all quadrats on the transect. The average cover for the Great Pond estuary as a whole was determined by averaging the percentage cover on all transects.

To obtain wet weight estimates of the standing crop of each of the dominant species, plants were removed from square meter quadrats with one hundred percent cover. The excess water was removed from the plants by draining and air drying for one hour. The quadrat sample was then weighed. For each species the weight of plants at 100 percent cover was multiplied by percentage cover of the species to obtain an actual standing crop estimate for the quadrat.

The 26 species studied in detail represented over seven-eighths of the total benthic crop of plant material present in the estuary at any season. Hence, the instantaneous biomass for all species measured was considered a reasonable estimate of the apparent net plant production for each month of the survey.

Biotic surveys were run every week, but individual quadrats were visited once every two weeks. Water analyses were made monthly during 1952–53, but every fortnight during 1954. Detailed analyses were based on the 1954 data, while those for the previous year were used to interpret trends in the environment during the period of observations on the biota. Limitations of time prevented detailed synoptic analysis of physical, chemical and biological changes in 1952–53. In January and April of 1953 storm conditions prevented observations on all transects. However, the partial data are used. All data were transcribed to McBee "Keysort" punch cards.

Measuring Physical and Chemical Factors

Salinity.—In 1952–53 salinity measurements were made with the aid of a precision-calibrated specific-gravity hydrometer. Salinity was determined from specific gravity readings by using the average of three readings per sample. Glass and temperature corrections were applied, and chlorinity and salinity values obtained from Knudsen's tables (Knudsen-Oxner, 1946).

Samples taken with a water sampler were placed in thrice-flushed 100 ml. glass-stoppered reagent bottles, sealed with petroleum jelly and inverted in storage. Measurements with the hydrometer were made the following day when all samples had reached room temperature. In 1954 all salinity samples were titrametrically determined by the Knudsen silver nitrate method (Knudsen-Oxner, 1946) and the values expressed in parts per thousand (‰).

Water Temperatures.—Water temperatures were recorded in both years with the aid of a $-10°$ to $+50°$ Centigrade (C.), partial immersion, guarded thermometer graduated in tenths of a degree. Both surface and bottom water temperatures were taken with the aid of a water sampler. Direct sunlight and exposure to cold winds were avoided during the readings.

Density.—Density of the estuarine water was obtained by converting salinity and temperature data at atmospheric pressure to *in situ* density using Knudsen's tables (Knudsen-Oxner, 1946). The results were expressed in Sigma-t Units (σ_t) obtained from density figures by moving the decimal three places to the right and dropping the initial 1: thus density 1.0260 gm./ml. = σ_t 26.0.

Dissolved Oxygen.—The standard Winkler method (Amer. Pub. Health Assoc. *et al.*, 1946, 1955) was used to determine the partial pressure of dissolved oxygen in sea water. Examination of results indicated amounts of ferrous and nitrate salts were not great enough to affect the accuracy of the method. The results were expressed in milliliters of dissolved oxygen per liter (ml./L.).

pH Measurements.—Measurements of pH were made within three hours after sampling with a Beckman Model G pH meter.

Total and Inorganic Phosphorus.—Inorganic phosphorus was determined by a modification of the Deniges colorimetric, stannous chloride method (Truog and Meyer, 1929; Amer. Pub. Health Assoc. *et al.*, 1955). The modifications were: (1) use of low-phosphate sea water for the preparation of standards to eliminate salt error and, (2) the use of a sea-going colorimeter, called the electric eye photometer (Ford, 1949). Total phosphorus was determined by a method after H. W. Harvey (1948) and the results expressed in microgram atoms of phosphorus per liter (μg-at P/L).

Nitrate and Nitrite.—Nitrite was determined according to a method first described by Ilosvay and later modified by Weston (1905). Nitrate was determined colorimetrically

using a strychnine reduction method of H. W. Harvey (1948). In both instances, the results are expressed in microgram atoms of nitrogen per liter (μg-at.N/L.).

Titration Alkalinity.—The method used is described in the American Public Health Association water analysis manual (1946, 1955). Both phenolphthalein and methyl orange alkalinity were determined and the results expressed in hydrogen ion equivalents.

Illumination.—Photometric measurements using a Leitz camera photometer were made seasonally to determine the minimum and maximum transparencies which could be expected in the estuarine waters. Data kindly provided by the Epply Co. of Newport, R. I., measured with an Epply pyroheliometer, gave total radiation in Langleys or gram calories per square centimeter per day (gm.-cal./cm.^{2}/day).

Current Measurements.—Both velocities and directions of the surface and subsurface tidal currents of Great Pond were measured and the values plotted for analysis. For determining surface currents, a standard 60 cm. meteorological balloon was attached directly to a galvanized sheet iron cross. For mid-depth current estimates the cross was suspended from the balloon by a 1 meter length stainless steel wire. The balloon was inflated just enough to buoy up the cross but not enough to cause appreciable wind drag. By releasing a number of current crosses from a given line and keeping track of their positions with time, the direction and rate for each could be obtained. In addition, a line of a half dozen current crosses were released and followed to obtain an estimate of the overall ebb and flood tide circulation for interpretative purposes. One analysis was made during a period of moderate southwest prevailing wind direction and another during a period of a fresh north-northwest wind.

Water Sampler.—The sampler consisted of four 100 ml. glass-stoppered bottles strapped to a wooden platform and separated by a wooden cross. A centered, two-foot-long upright member supported a 400 ml. plastic overflow chamber stoppered at both ends. The platform was weighted with a keel of six pounds of lead. The four reagent bottles were fitted with rubber stoppers with a pair of holes in each to accommodate the plastic tubing which led from the first through the last bottle in a series and finally into an overflow cylinder. The inlet tubing extended to the bottom and the outlet tubing was inserted just into the top of each bottle. This arrangement permitted a flow of water to move in succession through each of the four bottles and, finally, to fill the overflow cylinder. Normally a thin-walled, rubber air-escape tube could be attached to the top of the overflow cylinder and brought above the surface of the water. A hose clamp could then be closed on the free end and the air-filled sample bottles stoppered and lowered in a rack to any desired level in the water column without filling from unwanted levels. Upon opening the hose clamp water pressure would force the air from the bottles, fill them with sea water and in turn fill the overflow cylinder. In shallow water or at the surface insufficient water pressure is developed to operate the apparatus. To speed up the process, a 4 meter thick-walled rubber tube was attached to the top of the overflow cylinder and terminated with a bicycle pump with inverted pump washer. This arrangement provided enough suction without creating cavitation to fill the sampler in 20 seconds at any depth.

The first bottle in the series received the greatest degree of flushing and its contents were used for oxygen determination. The second sample was used for pH and titration alkalinity, the third for phosphorus, nitrate and nitrite, and the fourth for salinities. The water in the overflow chamber was suitable for temperature measurements since flushing tended to bring the chamber to water temperature. During the 1954 survey, a

weighted four liter glass pail, which could be filled at any level by pulling its stopper by an attached cord, was used to obtain water samples for all analyses except dissolved oxygen, pH, alkalinity and temperature. Samples for these were collected using the sampler described previously.

Data from Other Sources.—Precipitation, air temperatures and pressures as recorded at Nantucket Island, Massachusetts, were obtained from the U. S. Weather Bureau's climatological summaries, both national and regional.

Rochford's (1952) estuarine classification, based largely on salinity and bottom type, was used to characterize Great Pond. The zones, according to the system, are indicated in Table 1 and Figure 2. Great Pond estuary falls into Rochford's classification

TABLE 1

Hydrographic Zones in Great Pond Based Upon Differences in Salinity and Bottom Sediments

Zone	Sections	Stations	Bottom Types	Salinity ‰	
				Surface	Bottom
Neritic	none	1	coarse sand	28–31	30–32
Marine	I	4	coarse sand	28–31	29–31
Tidal	II, III	4A,6,6A,6B,7,7A,7B,8,8A,8B	firm sandy clayey silt	23–30	26–31
Transition	IV	9,9A,9B	soft silty sandy clay	12–30	20–31
Gradient	V, VI	10,11,12,12A,13,13A	soft silty sandy clay ooze	1–28	1–30
Fresh	VII	12E,13C	firm silty sand	<1	<1

of systems dominated by "tidal zone" characteristics without seasonal shifts in the positions of the zones. Most of the habitats in Great Pond are exposed to marine rather than brackish influences.

Seasonal Histories of the Principal Benthic Marine Plants

SEASONAL PERIODICITY OF GROWTH IN GREAT POND

From a check list of 135 species or varieties of benthic marine plants observed in Great Pond, the preliminary *seasonal histories*[2] of 89 were studied, but only 70 of these were suitable for quadrat analysis. Of the 70 suitable taxa, 26 of the more common forms were measured for seasonal growth studies. In Table 2 data for presence, growth, periods of maximum growth, and dormancy are given for each species. The species prominent at any one season are listed with information concerning their distribution in various sections of the estuary.

In the yearly cycle of growth in Great Pond the largest number of species and the maximum rate of growth occurred during the spring (Fig. 3, Table 2). The maximum standing crop occurred between June and early September but was represented by fewer species. A rapid decline in cover and number of species followed in September and October. By mid-autumn the warm season vegetation had greatly diminished and was replaced by the winter vegetation beginning in early November.

[2] In some areas, species of benthic marine plants may give rise to either or both of the alternating generations such as the sporophyte and gametophyte. In a field study, observation is made only on those generations which are most conspicuous. The term seasonal history was suggested by Taylor to mean only that portion of the life-history that may occur in a given area. For many species only one of the two generations, usually the sporophyte, was observed during the survey. With many thallophytes, the sexual and asexual generations have different seasonal periods of occurrence (Knight and Parke, 1931).

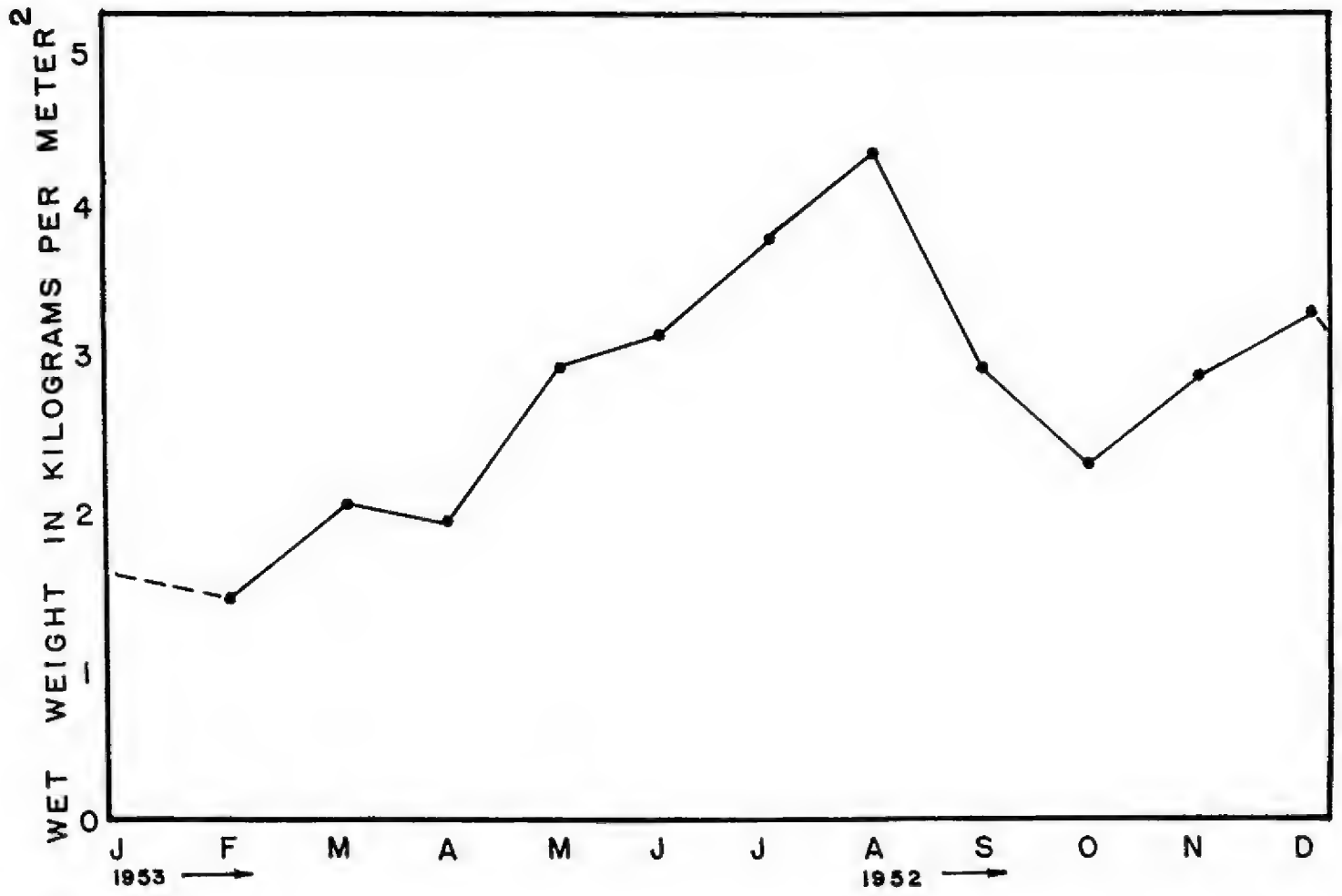


FIG. 3. Seasonal fluctuations in the total standing crop of benthic marine plants in Great Pond in 1952–53. Data are given in kilograms wet weight per square meter.

TABLE 2

Check List and Monthly Distribution of Benthic Plants in Great Pond, Mass. (after Taylor, 1957)
T = Trace Present; D = Dormant; G = Growth Indicated; M = Period of Maximum Standing Crop; ? = Uncertain.

	Months												Section of the Estuary which had maximum growth	Section of the Estuary which had minimum growth
	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.		
AQUATIC PHANEROGAMS														
Ruppia maritima L.	G	D	D	D	D	D	D	G	G	G	M	G	3–5	2
Zostera marina L.	G	G	D	D	D	D	G	G	G	G	M	G	1–4	5
XANTHOPHYTA														
Vaucheria thuretii Wor.	M	D	D	D	D	D	G	G	M	M	M	M	2–4	5
V. compacta	G	D	D	D	D	D	G	G	M	M	M	M	2–4	5
V. minuta Blum et Con.	G	D	D	D	D	D	G	G	M	M	M	M	2–4	5
V. coronata Nordst.	G	D	D	D	D	D	G	G	M	M	M	M	2–4	5
V. arcassonensis Dang.	G	D	D	D	D	D	G	G	M	M	M	M	2–4	5
V. intermedia Nordst.	G	D	D	D	D	D	G	G	M	M	M	M	2–4	5
CHLOROPHYTA														
Ulothrix implexa Kütz.	....	....	....	....	....	....	G	G	G	....	....	....	6	..
Enteromorpha clathrata (Roth) J. Ag.	G	G	M	M	M	G	M	G	....	M	G	....	2–4	5,6
E. compressa (L.) Grev.	....	.. .	....	....	....	. .	G	G	M	M	M	....	4,5	2,3
E. intestinalis (L.) Link	M	G	G	G	G	G	M	M	M	G	G	G	3,4	2,5
E. linza (L.) J. Ag.	M	M	G	G	G	G	M	G	M	G	M	G	1,2	3
E. plumosa Kütz.	M	G	G	M	....	....	....	G	M	G	G	G	3,4	5,6
E. torta (Mert.) Reinb.	....	....	....	....	....	....	M	G	G	M	G	G	2,3	4

TABLE 2—Continued

Check List and Monthly Distribution of Benthic Plants in Great Pond, Mass. (after Taylor, 1957)
T = Trace Present; D = Dormant; G = Growth Indicated; M = Period of Maximum Standing Crop; ? = Uncertain.

	Months												Section of the Estuary which had maximum growth	Section of the Estuary which had minimum growth
	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.		
Monostroma oxyspermum (Kütz.) Doty	....	G	M	G	G	....	G	G	G	M	....	....	5,6	..
Ulva lactura L.	G	G	G	M	G	G	M	M	M	M	G	G	1–3	4,5
Ulva lactuca var. *latissima* (L.) De Cand.	M	M	G	G	G	G	G	G	M	M	M	G	4,5	2,3
Ulva lactuca var. *rigida* (C. Ag.) Le Jolis	M	M	G	G	G	G	G	G	M	M	M	G	1	..
Chaetomorpha aerea (Dillw.) Kütz.	G	G	G	G	G	G	G	M	M	M	G	G	1	..
C. linum (Müll.) Kütz.	G	G	G	G	....	....	M	M	G	G	....	....	5	3
Cladophora gracilis (Griff. ex Harv.)Kütz. F. *tenuis* Farl.	M	M	M	G	....	....	G	G	G	M	G	G	3,4	2,5,6
C. refracta (Roth) Kütz.	G	M	G	....	....	G	G	M	M	G	....	....	4–6	..
C. rudolphiana (C. Ag.) Harv.	....	....	....	....	....	....	G	G	G	G	G	G	4–6	..
Rhizoclonium riparium (Roth) Harv.	....	....	....	....	....	....	G	M	M	M	G	....	4–6	..
PHAEOPHYTA														
Ectocarpus confervoides (Roth) Le Jolis	M	M	?	?	G	G	?	G	M	?	?	....	2	4
E. siliculosus (Dillw.) Lyngb.	?	?	?	M	G	G	G	M	G	G	G	....	2	5
Giffordia mitchellae (Harv.) Hamel	G	M	M	G	?	G	G	?	M	G	?	G	1	2
Sphacelaria cirrosa (Roth) C. Ag.	M	M	G	....	....	....	G	G	M	M	G	....	1	2
Ralfsia verrucosa (Aresch.) J. Ag.	G	M	M	M	G	G	G	M	M	M	G	G	1	2
Leathesia difformis (L.) Aresch.	....	....	....	....	....	....	....	....	....	M	....	....	1	..
Acrothrix novaeangliae Taylor	....	....	....	....	....	....	....	....	M	G	....	....	2	..
Stilophora rhizoides (Ehrh.) J. Ag.	T	T	M	M	G	G	G	G	M	M	G	G	3,4	2,5
Desmarestia viridis (Müll.) Lamour.	....	....	....	....	....	....	M	M	G	G	....	....	2	1
Striaria attenuata (C. Ag.) Grev.	....	....	....	....	....	....	....	....	M	....	....	....	2	..
Petalonia fascia (Müll.) Kuntze	....	....	G	M	G	G	M	M	G	G	....	....	1	2
Punctaria latifolia Grev.	....	....	G	M	G	G	M	M	G	....	....	....	1	4
P. plantaginea (Roth) Grev.	....	....	G	G	G	G	M	M	G	G	....	....	1	..
Scytosiphon lomentaria (Lyngb.) J. Ag.	....	....	G	G	G	G	G	G	G	G	G	....	1,2	3,4
Dictyosiphon foeniculaceus var. *americanus* Coll.	....	....	....	....	....	....	M	M	M	G	....	....	2,3	4
Chorda filum (L.) Lamour.	....	....	....	....	....	....	M	M	G	....	....	....	1	2
Fucus spiralis L. (typical)	M	M	M	M	G	G	M	M	M	M	D	D	1	2,3
F. vesiculosus L.	M	M	M	M	G	G	M	M	M	M	D	D	1	2,3

TABLE 2—Continued

Check List and Monthly Distribution of Benthic Plants in Great Pond, Mass. (after Taylor, 1957)
T = Trace Present; D = Dormant; G = Growth Indicated; M = Period of Maximum Standing Crop; ? = Uncertain.

	Months												Section of the Estuary which had maximum growth	Section of the Estuary which had minimum growth
	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.		
Sargassum filipendula C. Ag.	M	G	D	D	D	D	D	M	M	M	M	M	1	2
RHODOPHYTA														
Bangia fuscopurpurea (Dillw.) Lyngb.	....	....	....	....	G	M	M	G	....	....	....	....	1	4
Porphyra leucosticta Thur.	....	....	....	G	G	M	M	G	G	....	....	....	1	4
Nemalion multifidum (Web. et Mohr.) J. Ag.	....	....	....	T	T	T	....	....	G	M	T	....	1	..
Gelidium crinale (Turn.) Lamour.	M	G	....	....	....	....	....	....	G	M	M	M	1	..
Corallina officinalis L.	M	G	D	D	D	D	D	G	M	M	M	M	1	..
Fosliella lejolisii (Rosen.) Howe	....	....	....	....	....	....	G	G	G	G	G	G	1,2	3,4
Agardhiella tenera (J. Ag.) Schm.	G	D	D	D	D	D	D	G	G	G	M	M	3,4	1,2,5
Hypnea musciformis (Wulf.) Lamour.	G	....	....	....	....	....	....	....	....	....	....	M	1	2
Gracilaria verrucosa (Huds.) Papenf.	M	M	G	G	G	G	G	M	M	M	M	M	2,3,4	1,5
Chondrus crispus (L.) Stackh.	M	G	G	D	D	D	D	G	M	M	M	M	1	..
Champia parvula (C. Ag.) Harv.	G	....	....	....	....	....	....	....	M	M	M	G	1	2
Lomentaria baileyana (Harv.) Farl.	G	G	....	....	....	....	....	....	....	M	M	M	1,2,3	4,5
Callithamnion byssoides Arn.	....	....	M	G	G	G	M	G	G	G	....	....	1	2
Ceramium rubrum (Huds.) C. Ag.	M	M	M	D	D	D	M	G	G	G	G	G	1	2
C. rubrum var. *proliferum* Harv.	M	M	G	D	D	D	D	M	M	M	M	M	3	4
Griffithsia globulifera Harv.	G	G	....	....	....	....	....	....	....	....	....	G	1	2
Spyridia filamentosa (Wulf.) Harv.	M	D	D	D	D	D	G	G	G	M	M	M	2–4	1,5
Grinnellia americana (C. Ag.) Harv.	G	....	....	....	....	....	....	....	....	G	G	M	1,2	3
Dasya pedicellata (C. Ag.) C. Ag.	G	G	G	....	....	....	....	....	....	....	....	G	3	1,2
Bostrychia rivularis Harv.	....	....	....	....	....	....	....	....	....	....	M	M	4	5
Chondria baileyana (Mont.) Harv.	G	....	....	....	....	....	....	....	....	G	G	M	1,2	3
C. sedifolia Harv.	....	....	....	....	....	....	....	....	....	....	G	M	1	2
C. tenuissima (Good.)														
C. tenuissima (Good. et Woodw.) C. Ag.	....	....	....	....	....	....	....	....	....	....	G	M	1	2
Polysiphonia harveyi var. *arietina* (Bailey) Harv.	G	G	G	G	....	....	....	....	M	M	M	G	2	3–5
P. novae-angliae Taylor	G	G	G	G	G	G	G	G	M	M	G	G	1	..
P. denudata (Dillw.) Kütz.	M	D	D	D	D	D	G	G	G	G	G	M	3	4

The standing crop of winter vegetation (Fig. 3) was smaller than that of the spring and early summer. In the late spring period summer and winter vegetation elements were observed growing side by side (Figs. 4, 5, 6; Table 2). By May or June the winter populations had ceased active growth or had begun to disappear. Reproduction, however, continued until these populations disappeared in late May or June.

Thus the 1952–53 data show two distinct major sequences in the seasonal vegetation of Great Pond, a cold and a warm season group. There are two major periods of decline and decay; one in June to early August (death of the winter-spring populations) and another in late September and October (death of the summer populations). Both periods of decline represent a peak occurrence of epiphytes and animal grazers. There is also evidence for considerable bacterial activity. The end of the first period in early August is more noticeable when blades and stems of *Zostera* and *Ruppia* become detached and are driven up on the beaches by wave action. Here these plants decay and create a general nuisance to man. However, estimates show the amount of debris belonging to phanerogams in Great Pond to be less than one sixth of the total plant material present (Figs. 5, 7). Eel grass probably constitutes a much larger fraction of the plant communities on the coast where dense beds have returned since the great blight of the early thirties (Dexter, 1953).

Those species of benthic plants most common in the winter vegetation, with initial growth in November and December, included *Ectocarpus siliculosus, Petalonia fascia, Punctaria latifolia, P. plantagineae, Scytosiphon lomentaria,* and the perennial fucoids. New plants were produced sporadically all winter and spring by these species. By June

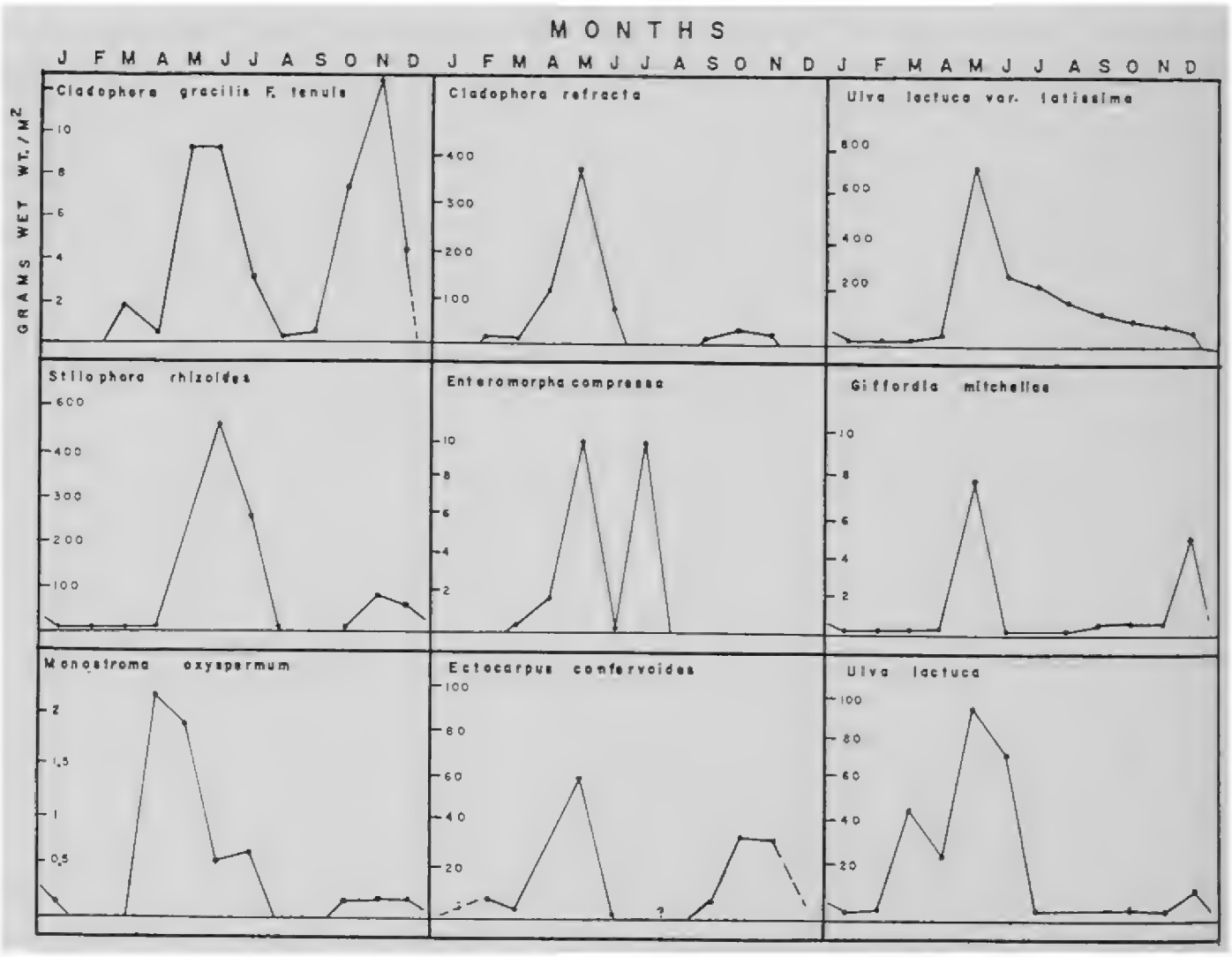

MONTHS
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
GRAMS WET WT./M2
Cladophora gracilis F. tenuis
Cladophora refracta
Ulva lactuca var. latissima
Stilophora rhizoides
Enteromorpha compressa
Giffordia mitchelliae
Monostroma oxyspermum
Ectocarpus confervoides
Ulva lactuca

FIG. 4. Standing crops of some benthic plants dominant in the spring and fall periods in 1952–53. Data are given as grams wet weight per square meter.

growth was generally very limited and only certain dormant persistent forms carried these species through the warm summer and fall months. In midwinter, usually by January, *Bangia fuscopurpurea* and *Porphyra leucosticta* made their appearance and flourished for a few months. By May only an occasional plant remained.

The spring vegetation in Great Pond appeared in March but most of the plant species were waning or gone by May or June. The list of species included ephemeral, short-growing-season species such as *Acrothrix Novae-angliae, Chorda filum, Desmarestia viridis, Dictyosiphon foeniculaceus* var. *americanus, Stilophora rhizoides, Striaria attenuata,* and *Nemalion multifidum,* as well as various species of *Cladophora, Enteromorpha, Monostroma,* and *Ulva.* The greens usually reappeared or showed another increase in abundance in the fall period. The sea grasses, *Zostera marina* and *Ruppia maritima* showed initial growth in mid and late spring but did not reach their peak growth until summer. The summer plant populations included the sea grasses which began initial growth in late spring. The most common algae species among these were *Enteromorpha compressa, Ulva lactuca* and its two varieties, *Agardhiella tenera, Gracilaria verrucosa, Ceramium rubrum* var. *proliferum, Hypnea musciformis, Spyridia filamentosa,* and a number of species of *Dasya, Ceramium, Champia, Lomentaria* and *Polysiphonia.*

In the fall, there was a reappearance and renewed growth of some species which grew in the spring. The list includes mostly greens such as the various species of *Enteromorpha, Ulva, Cladophora,* and *Monostroma,* and the brown *Stilophora rhizoides.* Between September and November no really new additional species appeared in Great

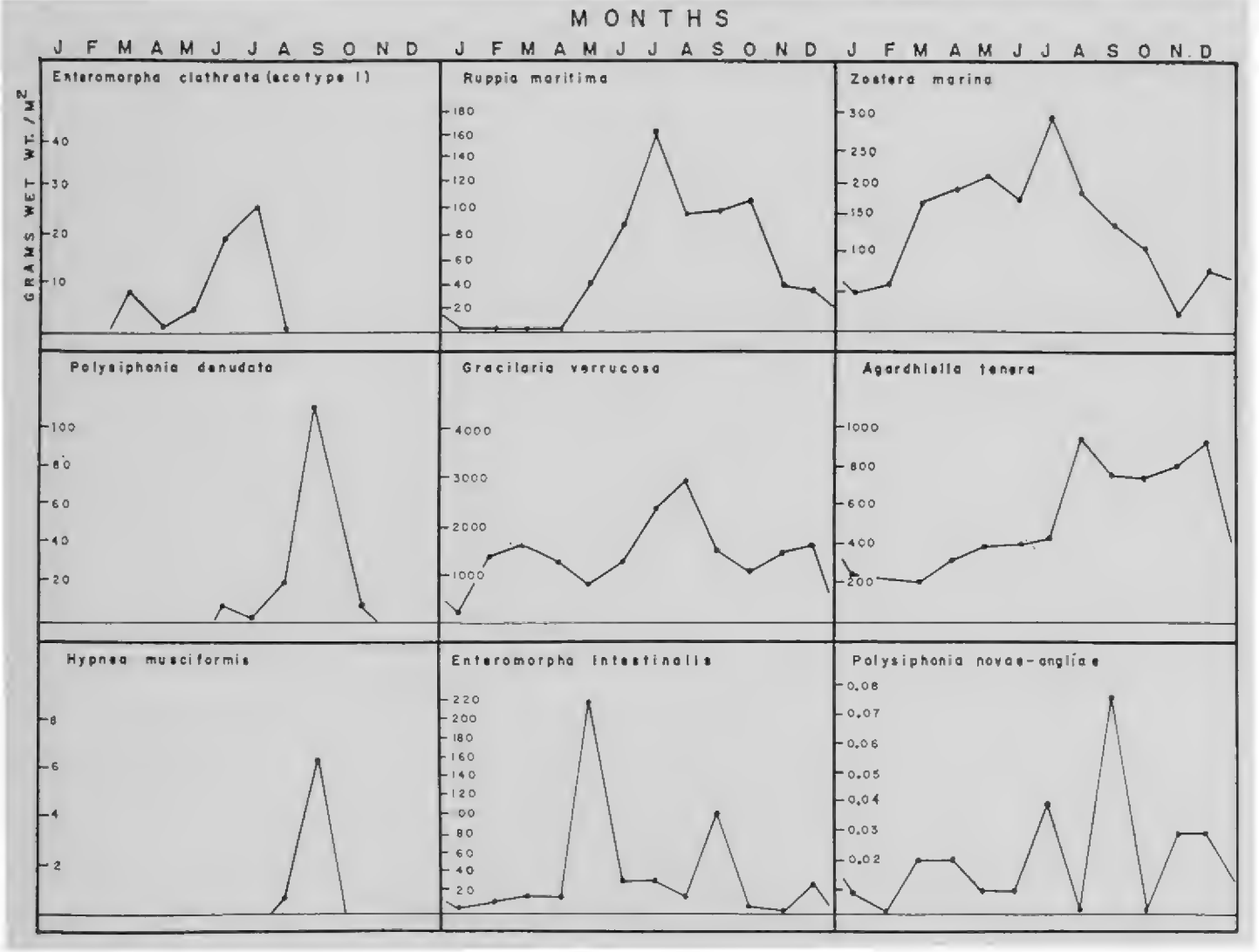

MONTHS
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
GRAMS WET WT. / M²
Enteromorpha clathrata (ecotype 1)
Ruppia maritima
Zostera marina
Polysiphonia denudata
Gracilaria verrucosa
Agardhiella tenera
Hypnea musciformis
Enteromorpha intestinalis
Polysiphonia novae-angliae

FIG. 5. Standing crops of some dominant species appearing in spring and summer, early spring through fall, and late spring through fall. Data are given in grams wet weight per square meter.

Pond. The winter plant communities generally appeared year after year, in late October along the coast and in early November in the estuaries.

For further details on the seasonal histories of benthic plants in Great Pond, see Table 2. The reader should be cautioned that these data represent measurements on the quadrats and do not include the occasional appearance in other parts of the estuary of other species. These seasonal histories are considered to be characteristic of an estuary rather than the open coastline.

Comparison of Seasonal Growth in Great Pond with Growth Regimes in Other Latitudes

Great Pond, at Latitude 41° N., as indicated in this study, has two major groups of plants each with growth at different seasons. Polar and tropical seas each have one dominant group with one growing season. Seas of intermediate latitudes are believed to be populated by more or less mixtures of warm and cold climate species. A brief review of studies concerning seasonal growth of marine plant communities from polar seas to the tropics shows the intermediate nature of southern New England plant communities.

In the Arctic, above Latitude 60° N., visual estimates of benthic marine plant growth suggest that there is only one seasonal growth period. Apparently growth only occurs during the short summer interval. Yet, reproduction may occur at other times of the year in some species. A review of these studies may be found in Fritsch (1945).

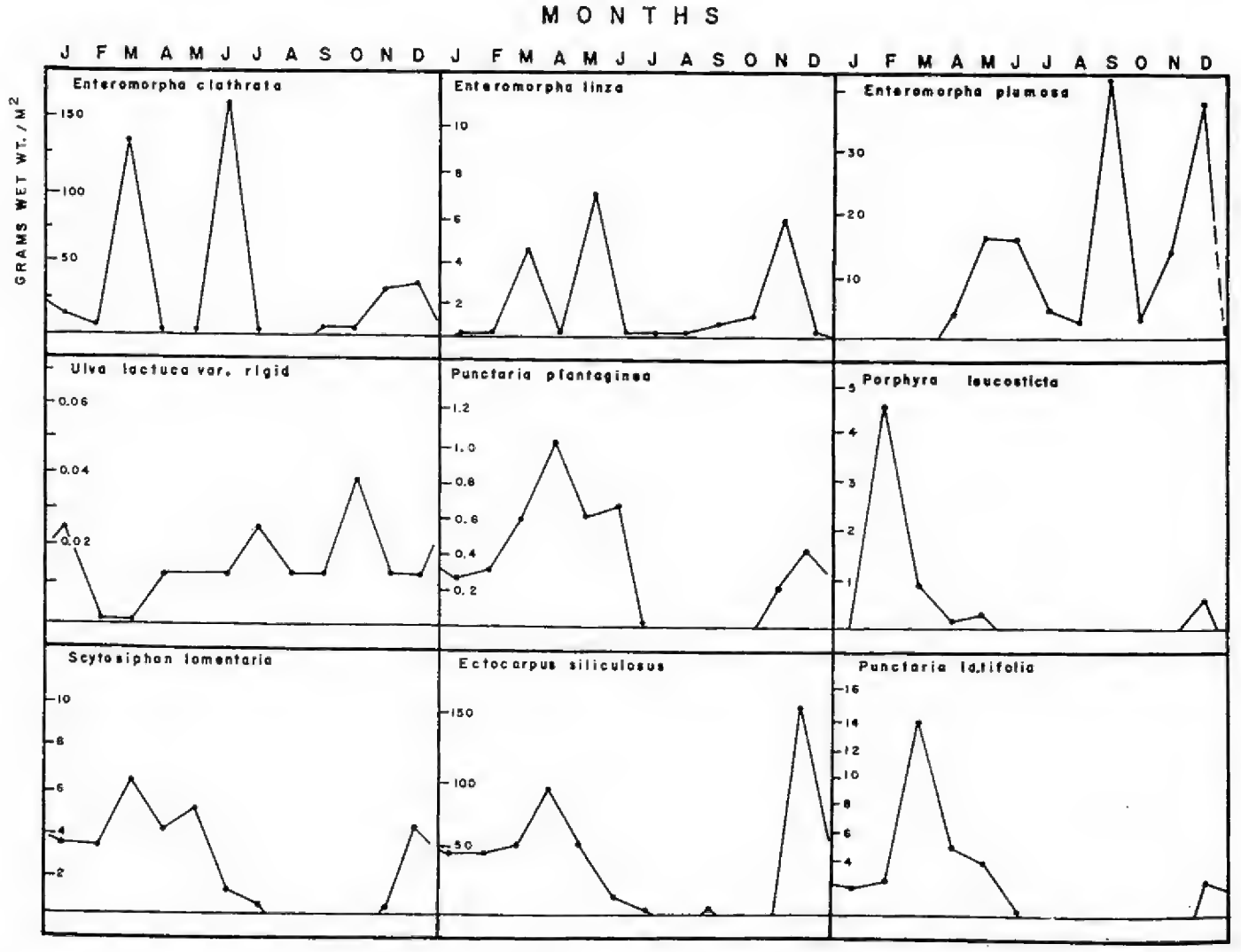

MONTHS
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
GRAMS WET WT./M²
Enteromorpha clathrata
Enteromorpha linza
Enteromorpha plumosa
Ulva lactuca var. rigid
Punctaria plantaginea
Porphyra leucosticta
Scytosiphon lomentaria
Ectocarpus siliculosus
Punctaria latifolia

FIG. 6. Standing crops of some benthic plants seasonally dominant in the fall and winter period in 1952–53. Data are given in grams wet weight per square meter.

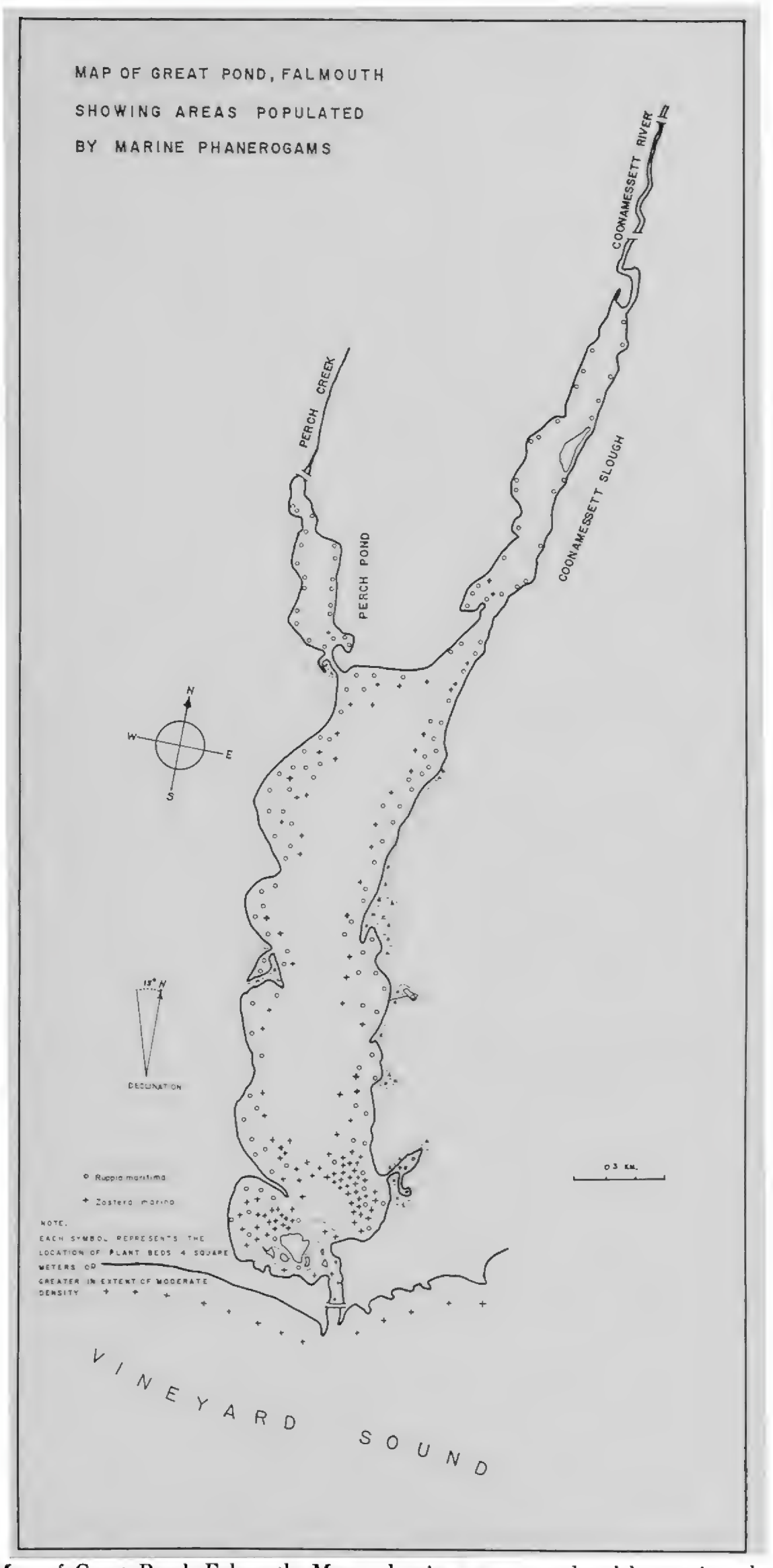


FIG. 7. Map of Great Pond, Falmouth, Mass., showing areas populated by marine phanerogams.

In boreal waters, MacFarlane (1952) reported a predominance of spring growth for the important commercial kelps and in Irish moss along the coast of Nova Scotia. These quantitative data are for open coastal water rather than protected or estuarine situations. Bell (1927) and Bell and MacFarlane (1933) provided visual estimates of a less prominent summer-growth group. No information appears to be available on winter growth for the area.

Bermuda, at Latitude 32° N., has really only one major seasonal growth group and possibly two minor ones (Bernatowicz, 1950, 1952a, 1952b). Only three winter species, *Callithamnion corymbosum*, *Scytosiphon lomentaria*, and *Sphacelaria tribuloides*, grow in those waters. Six annuals with short growth seasons appear in the spring but the bulk of the vegetation persists the year around. The maximum growth period for most species is in May and June. Bernatowicz's data are for quiet, protected habitats and hence may be readily compared with the Great Pond data. Results of studies in the Mediterranean by Feldmann (1937) and Funk (1927, 1954) suggest a similar seasonal growth aspect to that reported from Bermuda.

According to an early report by Svedelius (1906) the tropics may have only one major seasonal growth period. Presumably growth is maximum in winter and early spring at Ceylon.

Local Distribution in the Estuary

Standing crop totals for the commonest species (Figs. 4, 5, 6, 7; Table 2) clearly indicated that in Great Pond the bottom of the entire major basin (transects 6 through 9 sections II-IV, Fig. 2) supported the largest accumulation of benthic marine plants. In comparison, the intertidal areas of both basin and riprap supported a relatively negligible amount. The "gradient" zone was scantly populated by attached plants which occurred on the few sandy shoals and on the embankments of the sloughs. Some species populations showed a seasonal change not only in growth but in their local distribution within the estuary. In the cooler months these species tended to populate more brackish water in the upper basin and in the sloughs. Other species showed no such change in distribution.

One example, *Stilophora rhizoides* (Fig. 8) was typical of species with changing distributions, whereas others such as *Petalonia fascia* showed no such change. *Stilophora rhizoides*, an annual (Fritsch, 1945), was found somewhere in the estuary, at least as an occasional plant, during all seasons of the year. There were two seasonal periods of marked abundance alternating with periods of scarcity. In November and December of 1952, the populations of this species occupied an area in the middle and upper portions of the major basin (sections III and IV, Figs. 2, 8). A few plants were found just inside the entrance to Perch Pond Slough (transect 13, section V, Fig. 2). By February, no plants were found in any of the quadrats and only an occasional one was found elsewhere in the estuary.

In April a significant reappearance of *Stilophora rhizoides* occurred just inside the mouth of the Coonamesset Slough (section V, transect 10, Figs. 2, 8). During May, the species became conspicuous over the central and upper portions of the major basin (sections III and IV, transects 7–9).

In June the population in the upper end of the basin was noticeably diminished (section IV, Figs. 2,8). In contrast an increase in abundance occurred at the seaward end of the estuary (sections II and III, including transects 6 and 7). By July the plants

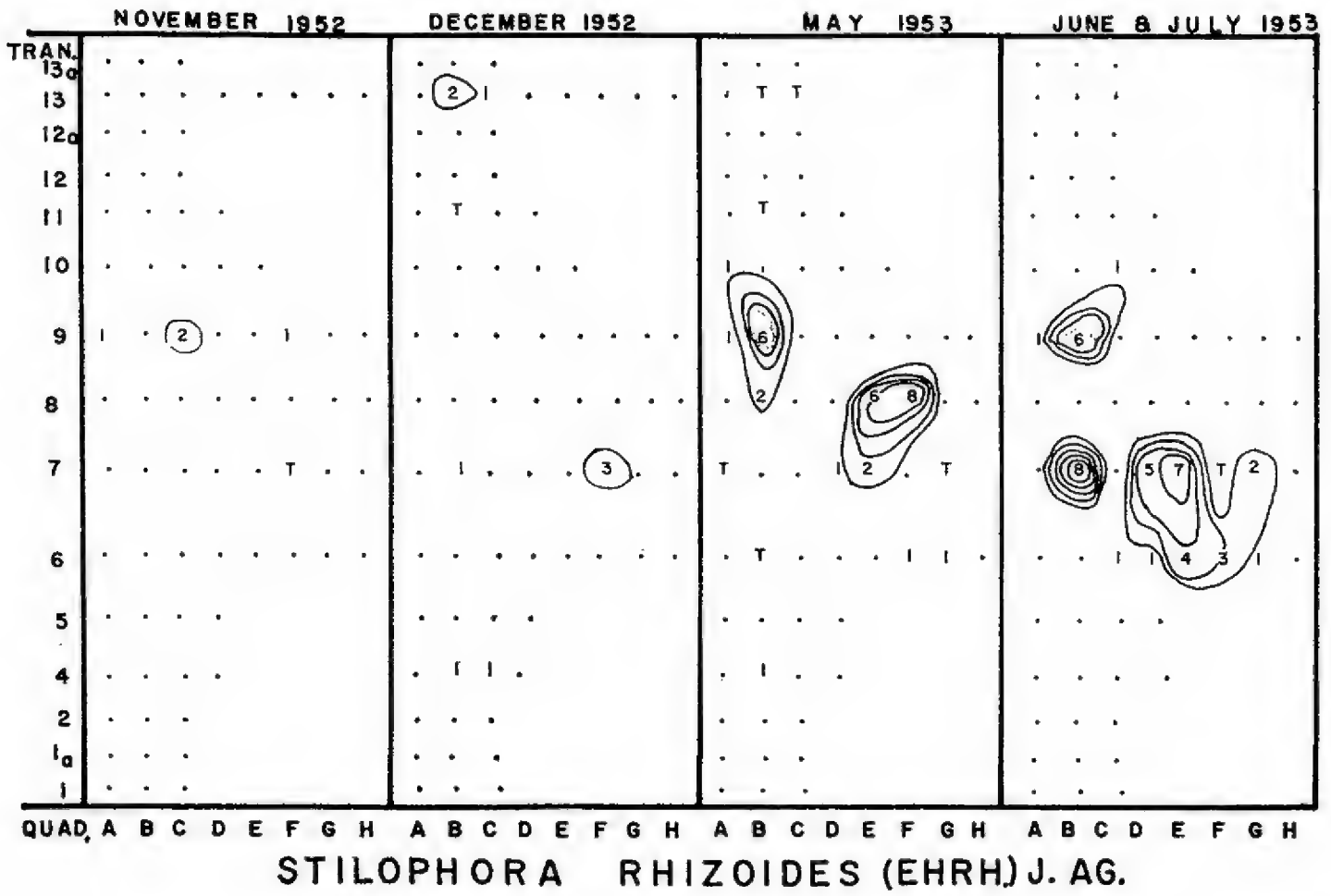


FIG. 8. Seasonal distribution and percent cover of *Stilophora rhizoides* in Great Pond in 1952–53. The graph shows transects 1 through 13 including transects in both sloughs. T indicates a trace. A dot indicates absence of plants. A number indicates the percentage cover of plants where 1=10 percent. Relative length of each transect is suggested by the length of each line of quadrats. Each dot on the riprap transects 1, 1A, and 2 represents four 25-centimeter-square quadrats. The number of quadrats is the sum of dots and numbers.

Species population isopleths indicate the plant's density in the estuary at four selected periods of the year. Isopleths are drawn at intervals: 15%, 30%, 45%, 60%, 75%, and 90%.

found at the upper end of the major basin in section IV were scarce, dying and heavily epiphytized. A fair abundance of somewhat healthier plants was found toward the lower end of the basin (section II, transect 6, Fig. 2). During August and September individual plants were rarely seen in the estuary and none within the measured quadrats. The few occasional plants found in late summer were in fairly saline habitats near the mouth of the estuary (section II, transect 6, Fig. 2). A similar history was found for *Gracilaria verrucosa* as shown in Figure 9.

CHANGES FROM ONE YEAR TO THE NEXT IN SPECIES COMPOSITION AND ABUNDANCE

Since the present quantitative vegetation survey was begun in July of 1952 and terminated in August 1953, direct comparisons between 1952 and 1953 were possible for the months of June, July and August. Spot checks on some quadrats were made in 1954 and some cursory inspections at several seasons conducted in 1955 and 1956. Some species were either missing or had altered their positions in the economy of the estuary. Conspicuous by its absence was *Punctaria plantaginea* in the winters of 1954 and 1955. Not even an occasional plant appeared in or near the entrance of Great Pond. The species *Punctaria latifolia* was not nearly as abundant in 1954 and 1955 as the previous winter, 1952–53. Some *Zostera marina* beds failed to produce leaves in 1954–55 becoming less abundant. The sea grass, *Ruppia maritima*, showed a distinct increase in

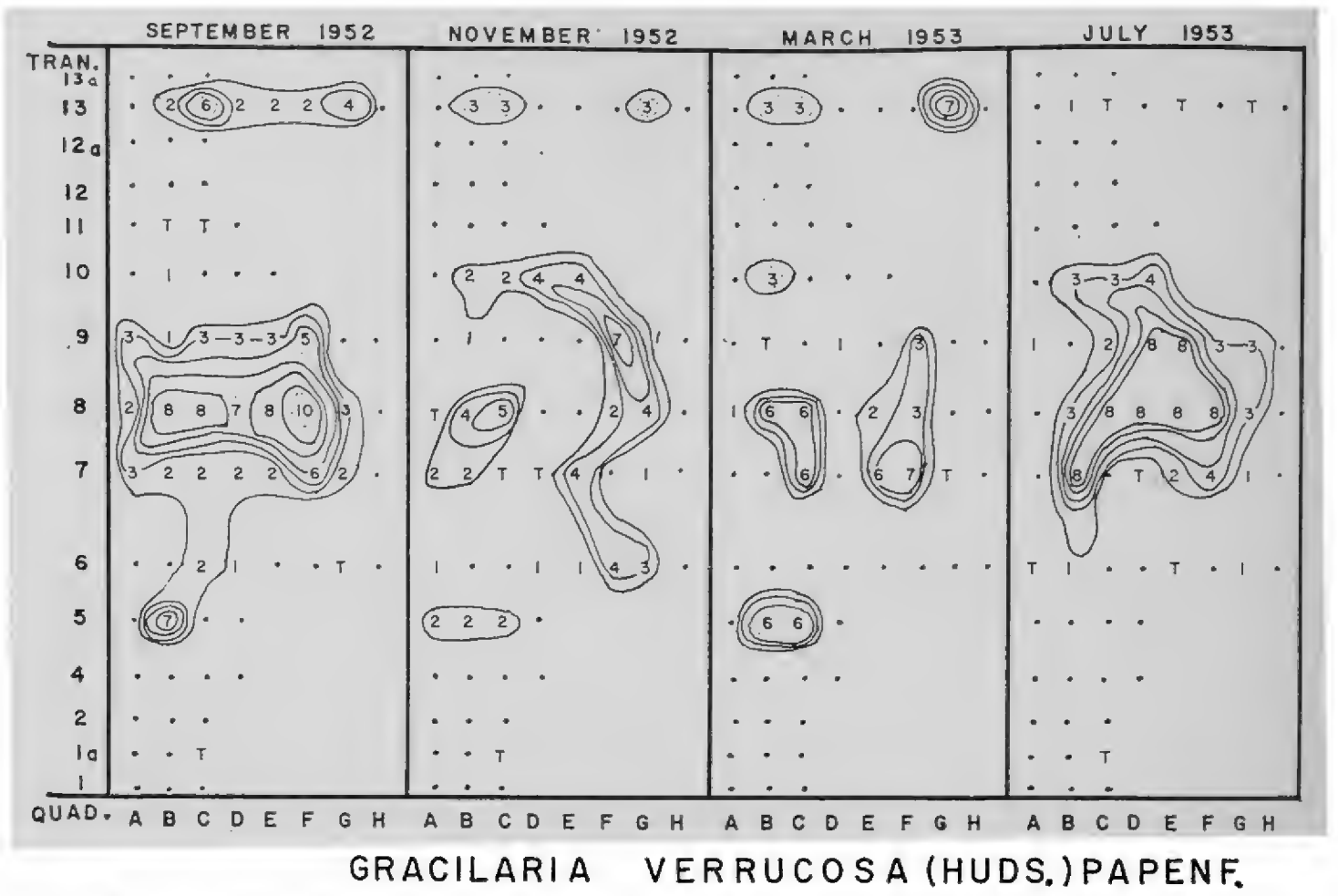


FIG. 9. Seasonal distribution and percentage cover of *Gracilaria verrucosa* in Great Pond in 1952–53. Isopleth interval is 15 percent. Legend is the same as for Figure 8.

1954–55 especially in areas occupied largely by Zostera in 1952–53. The species accumulating the largest biomass in Great Pond was *Gracilaria verrucosa*. This form was abundant in 1952, less abundant in 1953 and was further reduced in 1955. The alga, *Gelidium crinale*, absent for several years from the Woods Hole-Falmouth area, according to Taylor (personal communication), had appeared as a conspicuous but narrow intertidal zone 3 cm. wide on the jetty. By the winter and spring of 1955, very little of this population remained. In 1956, *Gelidium* seemed to be reclaiming ground lost in 1955 but diminished after the more severe winter of 1957. The species *Bostrychia rivularis* was first observed in July 1952. By the summer of 1956 no plants could be found anywhere in the estuary.

Overseason Persistence of Summer and Winter Species

An opportunity to study the winter persistence of some species was afforded during the seasonal growth survey. Branched basal portions of the previous season's thalli of *Gracilaria verrucosa*, which had persisted through the winter months, were observed to regenerate new, branched systems the following spring. During the winter period no intact, branched, basal portions of this species were observed along the exposed coast where holdfasts are commonly found. Dormant, branched portions of thalli may only occur in quiet, protected waters such as Great Pond.

In *Agardhiella tenera*, branched portions of the thallus likewise persisted over winter and in late spring produced new growth. In addition, small germlings of *Agardhiella* were found in late spring at the same time that regeneration was detected in the branched thalli of the previous growing season. The juvenile plants were seen only outside the estuary on pebbles and shells in the shoal water of Vineyard Sound. Apparently

Agardhiella over-winters as holdfast discs in coastal water and vegetatively in south shore tidal estuaries.

Solitary plants of *Nemalion multifidum*, an early summer annual, were observed in mid-winter attached to boulders below the intertidal zone. In contrast the early summer habitat was in the upper intertidal zone. Maximum luxuriance of this species occurred in late June. Unattached, branched portions of *Hypnea musciformis* were found in May apparently dormant, but viable, suggesting that these may regenerate after the winter. Some individuals of *Ceramium rubrum* passed the winter months mature, full-grown, and actively reproducing. The size and number of individuals were usually reduced suggesting very limited vegetative growth.

Seasonal Periodicity in Reproduction

Some observations of a general nature were made on the occurrence of reproduction in the seasonal histories of some species of benthic plants. Generally, conspicuous reproductive structures such as those developed in the Rhodophyta and Phaeophyta are present throughout the period of maximum luxuriance and continue into the waning phase. In *Polysiphonia novae-angliae*, *P. denudata*, *Champia pravula* and *Agardhiella tenera*, both the gametophyte and the sporophyte were present during the season of active growth. An increase in population usually was paralleled by an increase in the number of individuals bearing reproductive structures. A correlation between growth and reproduction for some species was also found in Bermuda by Bernatowicz (1952a). Smith (1947) found a correlation between spring tides and sporulation in *Ulva lactuca*. Evidence for similar periodic sporulation was obtained in Great Pond. Measurements were made on juvenile plant populations of *Ceramium rubrum*, *Petalonia fascia*, *Sargassum filipendula* and *Scytosiphon lomentaria*. In the study of *Scytosiphon*, for example, the juvenile plants were measured on four 25-centimeter-square plots on different, closely associated, rock surfaces at about the same intertidal exposure. The plants were very uniform in height. Within each plot less than one third of the height measurements exceeded the standard error for all plots. This evidence suggests that nearly all plants in each plot germinated at about the same time. Over a period of 20 days. the mean height of juvenile plants in each plot increased uniformly as shown in Table 3. Older plants

Table 3

The Mean Height of Juvenile Plants of *Scytosiphon Lomentaria* in Four Plots on a Jetty at Falmouth, Mass.
(Height in centimeters)

	Plot number			
	1	2	3	4
March 3	2.8	2.3	1.9	2.0
March 8	3.4	3.5	3.3	3.4
March 14	5.2	5.7	5.1	5.3
March 21	8.1	8.4	8.0	8.2

in all plots were significantly taller than the juveniles. Possibly the sexually mature plants in the population had responded to some rhythmic factor in the environment.

The study of the seasonal growth of benthic marine plants in Great Pond has provided measurements of a series of biological events. These events may be characteristic of other quiet water lagoons or estuaries in southern New England. The environmental factors causally related to these growth events are considered in the following chapter.

Effects of Environmental Factors on the Seasonal Growth of Benthic Plants

Those environmental influences which normally occur year after year may be separated from those which occur intermittently, irregularly, or rarely. Some of the regular influences found to be important are insolation, air and water temperatures, chemical properties of the water mass, tidal movements, the run-off waters from fresh-water streams, and the seasonal weather patterns of the region.

The irregular types of environmental influence include insolation in prolonged periods of clear skies, severe low temperatures, icing, unusual numbers of severe frontal storms, tropical hurricanes, prolonged emersion and immersion due to offshore or onshore winds, pollution by man, wholesale wasting diseases due to plant parasites (Dexter, 1953, Taylor, 1933) and unusually heavy grazing by a large year-class of some herbivorous animal (Lodge, 1948; Odum, 1953). During the course of the present survey, an evaluation of both regular and irregular factors was made.

Light, Temperature, and Seasonal Growth

The separate effects of light and temperature on plant growth may be provisionally separated in a field study since the annual temperature and light curves (Figs. 10, 11)

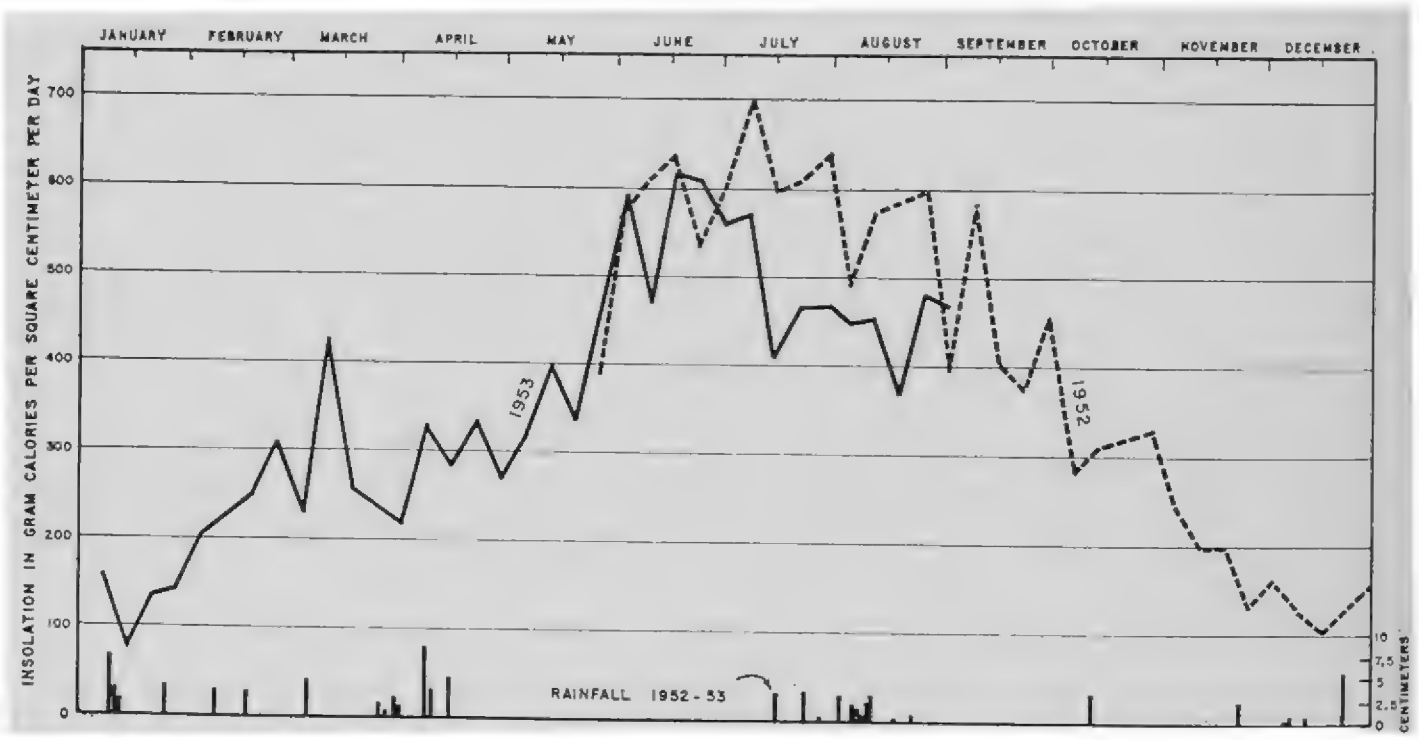


Fig. 10. Weekly average of total solar radiation at Newport, Rhode Island, 1952–53. The bar graph at the bottom of the figure indicates rainfall in centimeters.

show minima, maxima, rises and falls at different times. It is fully appreciated that interpretations of results are limited due to the many interacting variables on growth. These results reported here are thus tentative. Further experimental studies are needed to confirm the suggested relationships.

Overall benthic plant production in Great Pond during 1952–53 indicates that the largest standing crop developed between June and September with the maximum in August (Fig. 3). The minimum plant biomass occurred in January and February. These maxima and minima are associated with the maxima and minima in temperature and insolation (Figs. 10, 11) suggesting that these two factors play the leading role in the seasonal growth of benthic plants in Great Pond.

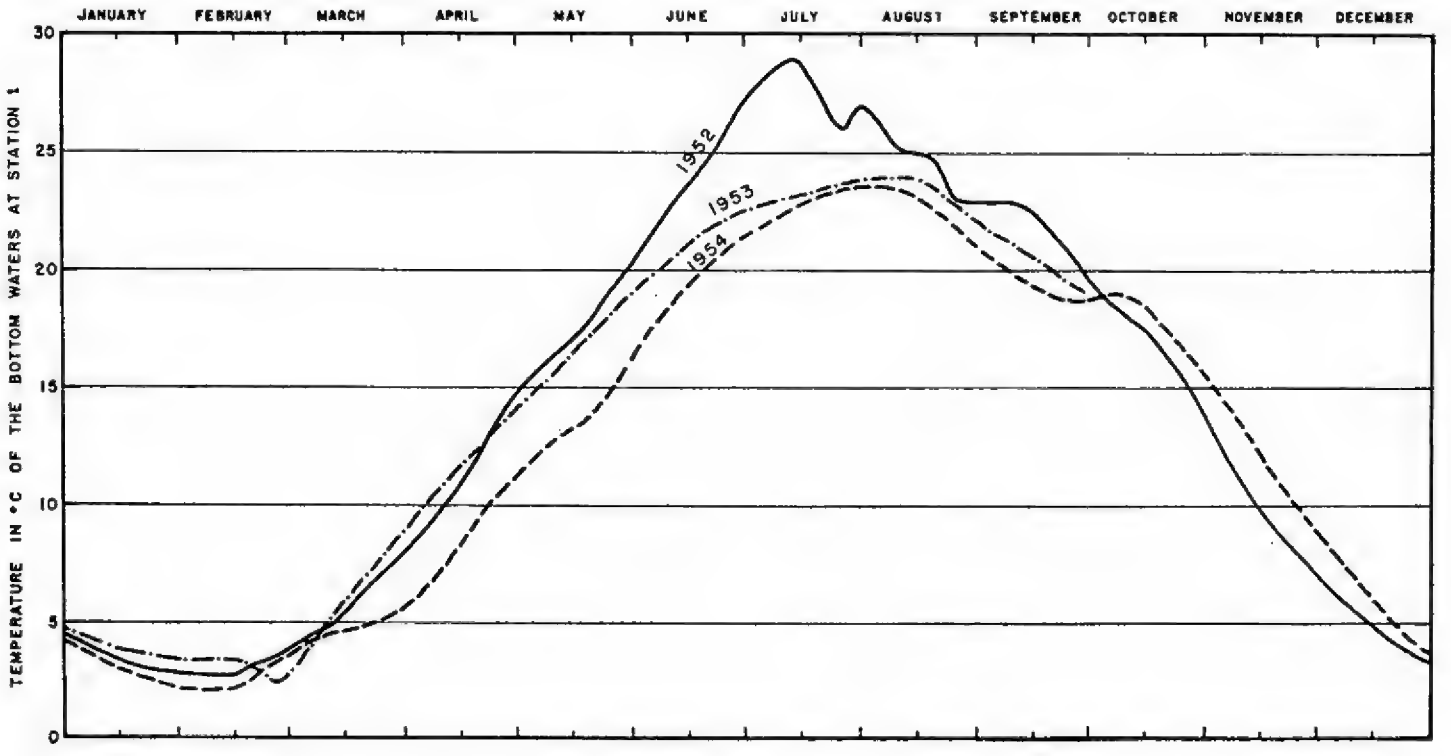


FIG. 11. Seasonal changes in the bottom water temperature in 1952–53 in the "neritic" zone (Figure 2) adjacent to Great Pond.

Late winter and early spring species including some short-growing-season ephemerals, (Fig. 6, Tables 2, 4) attained maximum population density in April and May and showed a marked reduction by June. Presumably these plants were adjusted for optimum net phytosynthesis at low temperatures and illumination. Plant species with maximum growth in the spring period were of two types. One showed irregular growth (see section on nutrients) through the season, i.e., *Enteromorpha compressa* (Fig. 4), while the other maintained a steady increase in growth, i.e. *Stilophora rhizoides* (Fig. 4). The latter type, growing in late spring (Table 5), is believed to be more dependent on light than temperature. Temperature effects are undoubtedly present. A more rapid weekly increase in light as compared with temperature supports this opinion (See Figs. 10, 11; compare the slopes of curves for April-June).

A different group of species attained maximum growth rates during June and early July (Fig. 5, Table 6) during the peak illumination period (Fig. 10). Other plants (Fig. 5, Table 7) grew best during the temperature maximum (Fig. 11) in August. These data suggest one group of species may be adapted for optimum net photosynthesis at maximal light and submaximal temperature while the latter group is adapted to maximal

TABLE 4

Standing Crops of Some Dominant Benthic Plants Occurring in Late Winter and Spring, 1952–53 (in Grams Wet Weight per Square Meter)

Species	March	April	May	June
Cladophora refracta	1.4	132.0	346.0	84.2
Enteromorpha clathrata	134.8	0.1	+	161.0
Enteromorpha intestinalis	17.9	12.9	228.0	30.8
Enteromorpha linza	4.3	0.0	6.9	0.0
Monostroma oxyspermum	0.0	2.2	1.9	0.5
Ectocarpus confervoides	6.4	?	62.0	2.4
Giffordia mitchellae	0.0	?	7.5	0.1
Ectocarpus siliculosus	49.5	93.9	49.5	8.9
Punctaria latifolia	14.0	5.4	3.9	0.1
Scytosiphon lomentaria	6.4	3.7	4.9	0.5
Ulva lactuca	48.2	22.6	98.7	77.2

temperature and submaximal light for this latitude. It should be pointed out that the few species listed in Table 6 are responsible for the largest fraction of the plant cover for the mid-summer period.

A small group of species, including plants with warm climate affinities, grew in Great Pond over September and into early October of 1952 (Tables 2, 8). The influence of light may have dominated other factors in its effect on growth. The fall off in light intensity was rather rapid in September and October (Fig. 10), but bottom water temperatures tended to fall more slowly (Fig. 11). There was a general reduction in standing crop of most species in the estuary in October (Figs. 3, 4, 5; Tables 2, 8) possibly associated,

TABLE 5

Standing Crops of Some Dominant Benthic Plants Occurring in the Late Spring Period, 1953
(in Grams Wet Weight per Square Meter)

Species	April	May	June	July	August
Cladophora gracilis f. *tenuis*	5.7	98.5	98.0	30.3	0.2
Enteromorpha intestinalis	12.9	228.0	30.8	33.2	13.1
Enteromorpha linza	0.0	6.9	0.0	0.0	0.0
Enteromorpha plumosa	3.8	16.7	16.3	4.6	3.0
Stilophora rhizoides	12.8	222.0	398.0	253.0	0.6
Ulva lactuca var. *latissima*	13.7	652.0	274.0	191.4	44.3

TABLE 6

Standing Crops of Some Dominant Benthic Plants Occurring in the Mid-Summer Period, 1952–53
(in Grams Wet Weight per Square Meter)

Species	April	May	June	July	August	September
Agardhiella tenera	350.0	124.0	406.0	464.0	989.0	785.0
Enteromorpha compressa	1.9	10.2	0.6	9.9	0.0	0.0
Gracilaria verrucosa	1,262.0	733.0	1,310.0	2,310.0	2,980.0	1,452.0
Ruppia maritima	+	35.4	34.0	161.0	96.9	98.5
Zostera marina	+	208.0	170.0	293.0	188.0	136.0

TABLE 7

Standing Crops of Some Dominant Benthic Plants Occurring in the Late-Summer Period, 1952–53
(in Grams Wet Weight per Square Meter)

Species	June	July	August	September	October
Enteromorpha intestinalis	30.80	33.20	13.10	107.00	6.74
Enteromorpha plumosa	16.30	4.57	3.02	47.30	2.38
Hypnea musciformis	0.00	0.00	0.35	6.91	0.00
Polysiphonia denudata	6.95	3.35	60.00	118.00	1.60
Polysiphonia novae-angliae	0.01	0.00	0.001	0.10	0.001

TABLE 8

Standing Crops of Some Dominant Benthic Plants Occurring in the Autumn Period
(in Grams Wet Weight per Square Meter)

Species	August	September	October	November	December
Cladophora gracilis f. *tenuis*	0.2	0.6	77.7	134.5	0.0
Cladophora refracta	0.0	22.7	41.1	29.3	0.0
Ectocarpus confervoides	?	9.3	30.6	29.7	?
Ulva lactuca	0.6	0.6	1.9	1.4	11.2
Monostroma oxyspermum	0.0	0.0	0.1	0.1	0.1

in part, with the decrease in light intensity. During the last two weeks of October bottom water temperatures dropped below 18° as the rate of cooling increased. Decreases in both temperature and light at this time may have accelerated the degradation of warm season plant populations.

A few plants, which grew in the spring, including *Cladophora gracilis* F. *tenuis, C. refracta, Enteromorpha clathrata, E. intestinalis, E. plumosa* and *Monostroma oxyspermum* (Figs. 4, 6; Tables 5, 8) showed renewed growth in the fall. Light intensities were similar in spring and fall during the periods of growth. Yet, water temperatures were several degrees higher in the fall for the same light intensity. Does this mean that light was the determining factor? Phytoproduction was much lower in the fall for these species populations. There is a possible explanation. In the spring light and temperature as well as photosynthesis and respiration were increasing. In the fall solar radiation and metabolism were decreasing.

In November, the species shown in Table 9 appeared to be dominant and by December had carpeted the estuary. Many of these cold season annuals had appeared along the open coast a week or two earlier. The difference in time of initial growth between

TABLE 9

Standing Crops of Some Dominant Benthic Plants Occurring in the Winter Period (in Grams Wet Weight per Square Meter)

Species	November	December	January	February	March	April
Ectocarpus siliculosus	?	152.000	44.600	42.600	49.500	93.900
Punctaria latifolia	?	2.460	1.800	2.480	14.000	5.450
Punctaria plantaginea	0.184	0.390	0.265	0.265	0.604	1.050
Scytosiphon lomentaria	0.145	4.000	3.040	2.940	6.440	3.680

estuary and coastal communities in 1952 may possibly be explained on the basis of the presence of higher temperatures (Fig. 12) within the estuary than along the coastal areas. By early November temperatures in both protected and exposed communities were below 18° C. The light intensity associated with early November (Fig. 10), the time of initial growth of these winter plant communities, was the same as that in March and April. Water temperatures in the spring period, however, were 5° C. lower (Fig. 11). Maximum growth was exhibited by these species in March and April (Fig. 6, Tables 2, 4). These data seem to indicate that the rôle of light was possibly more critical as related to growth than water temperature.

The only species which grew best during the winter temperature minimum in January and February of 1953, were *Bangia fuscopurpurea* and *Porphyra leucosticta* (Table 2). These plants grow well at or near freezing temperatures. The plants appeared while illumination increased from the winter minimum of less than 100 gm. cal./cm.^{2}/day on January 10th, 1953, to 300 gm. cal./cm.^{2}/day by mid February. Here is another example in which light intensity may have been more important than water temperatures. Many of the winter species present in Great Pond grow in summer in polar and boreal seas (See review by Fritsch, 1945). It is suggested from the above results that a study of boreal and polar benthic plant growth with respect to light and temperature may show the critical rôle of illumination at high latitudes.

NITRATE, PHOSPHATE AND SEASONAL GROWTH

From physiological studies (Gessner, 1955) it is known that the amounts of nitrate and phosphate available can regulate plant growth during periods of nutrient scarcity.

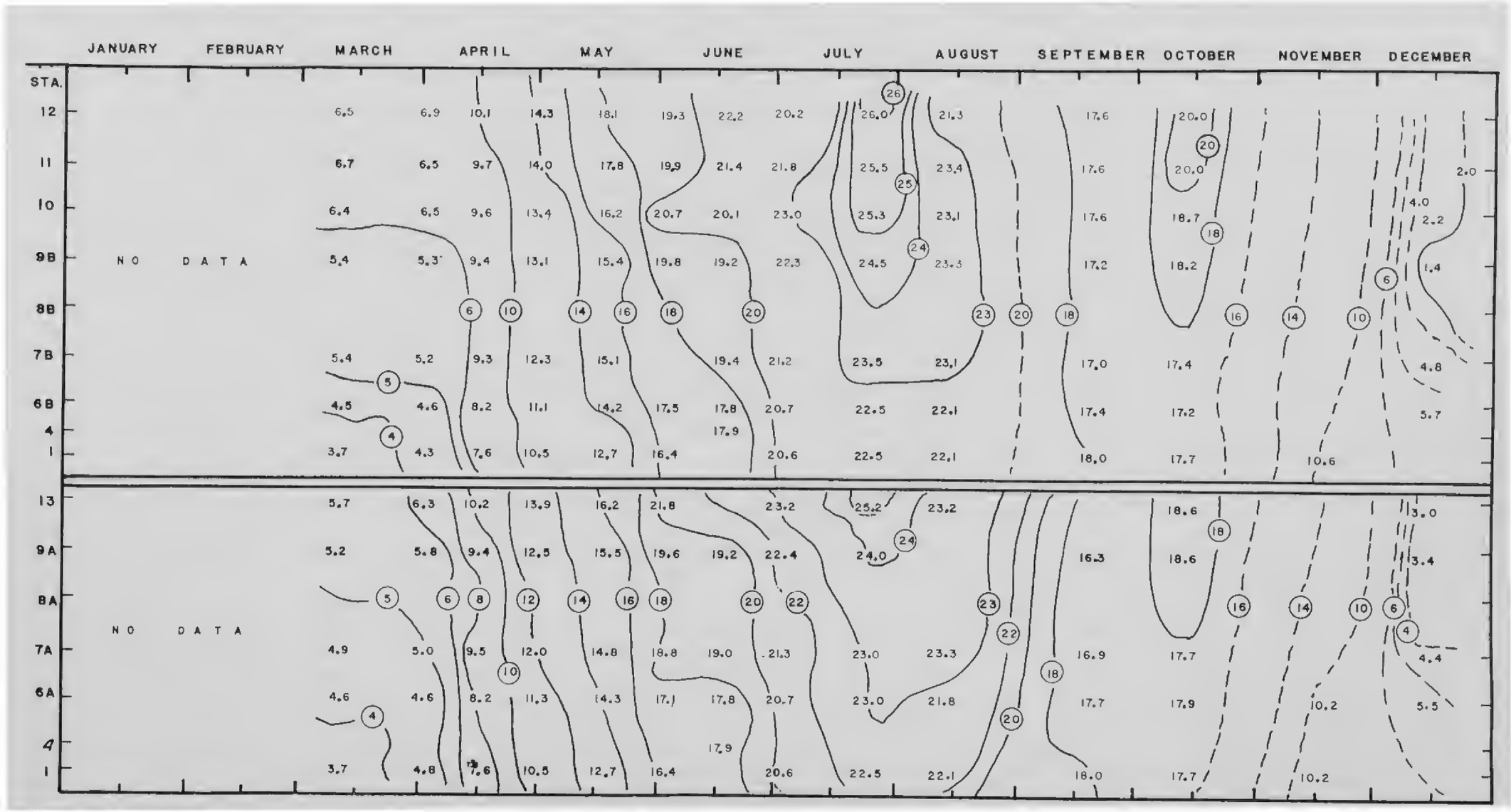


FIG. 12. Temperature in the bottom water of Great Pond, Falmouth in 1954 in degrees centigrade (C°).

In this and all subsequent frequency polygon projections of Great Pond data, two graphs are shown separated by a double line. The lower graph represents a section along the western side of the estuary including station 1 in Vineyard Sound and station 13 in Perch Pond Slough. The upper graph represents a section on the eastern side of the estuarine basin also including station 1 in the sound as well as stations 10 through 12 in the Coonamessett Slough. The two graphs provide a means of comparing the more swiftly moving tidal water of the eastern half of the basin with the more sluggish water of the western half.

Multicellular plants store large concentrations of nutrients in their extensive tissues (Vinogradov, 1953). In estuarine communities the available nutrients are in part supplied by regeneration from dead plants.

Evidence that nitrogen and phosphorus may limit growth in Cape estuaries is provided by a fertilization experiment (Pratt, 1950) conducted in Megansett estuary. Enriched fertilizer was dumped into the small embayment. Large excesses of nitrogen and phosphorus yielded blooms of phytoplankton, and masses of benthic plant growth fouled the shallow basin. Great Pond is like Megansett estuary with a similar geologic history.

In Great Pond there are low concentrations of nitrate (NO^3-N) and inorganic phosphate (PO^4-P) during the spring and fall periods (Fig. 13). One period of maximum

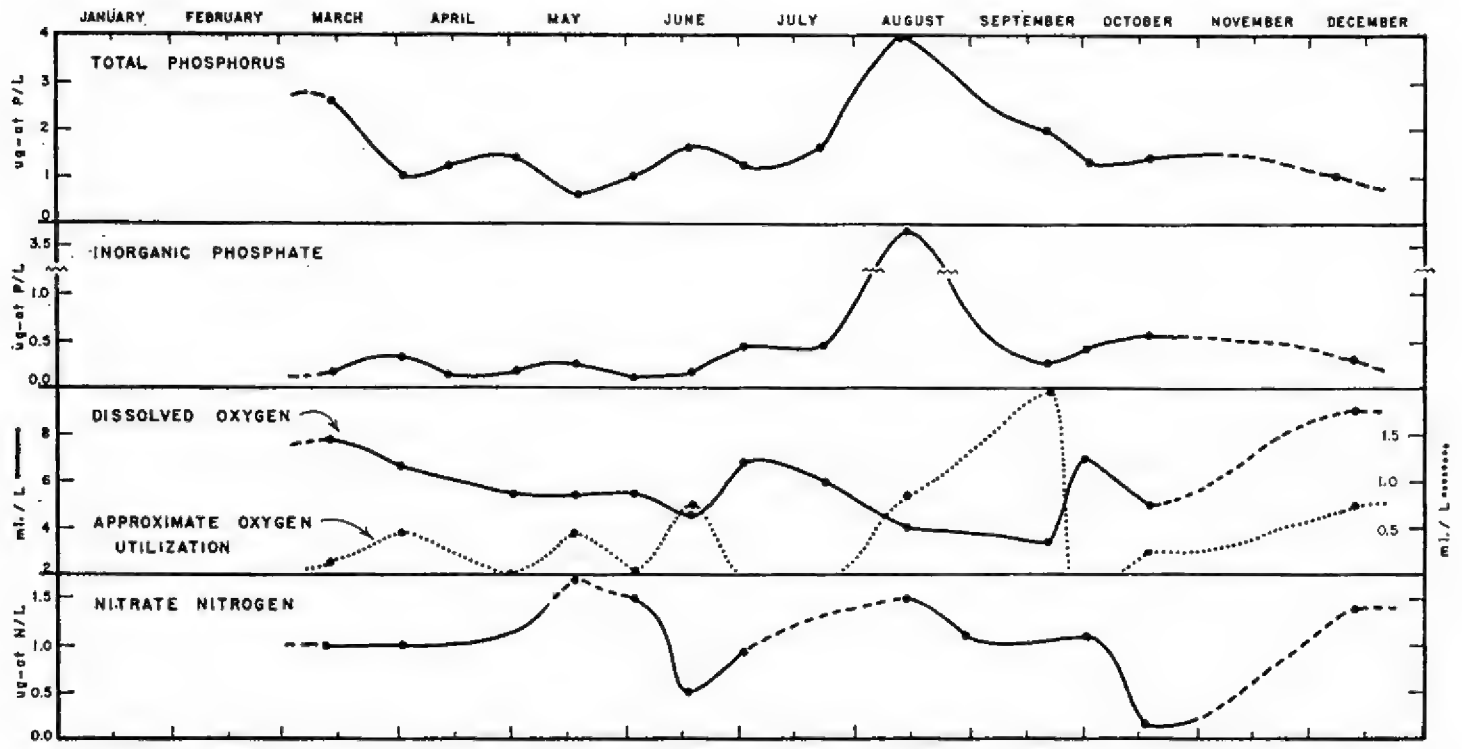


FIG. 13. Seasonal changes in total phosphorus, inorganic phosphate phosphorus, nitrate and dissolved oxygen in the bottom water of the "transition" zone (Figure 2) of Great Pond in 1954.

nutrient salt regeneration *in situ* within the estuary occurs in August, and minor ones occur in late fall and in the spring (Fig. 13). The spread and reduction in abundance of many benthic plant species seems to follow changes of phosphorus in spring and nitrogen in the fall.

Data for the seasonal fluctuations in the nitrogen cycle in Great Pond (Fig. 13, 14, 15, 16) furnish some evidence that nitrate may have been low enough in the bottom water to affect the growth of benthic plants in October. Measurements of nitrogen in October indicate that less than 0.4 μg-at. N/L were present in those sections (II–IV, Fig. 2; Table 2) of Great Pond where phytoproduction was high in other seasons. Concentrations of nitrogen and phosphorus were considered low when amounts were near or at limiting levels for unicellular algae under laboratory conditions (Ketchum 1939). During October a number of species, many of them dominants, exhibited drastic reductions in standing crops (Figs. 3, 4, 5; Tables 2, 8). Many plants terminated growth. The possibility that light and temperature play an important rôle here was discussed earlier. No new additions to the benthic vegetation were observed in October. Only two species *Cladophora gracilis* f. *tenuis* and *Ulva lactuca* var. *rigida* increased in standing crop. There was a delay in the appearance of winter species within the estuary (Fig. 6,

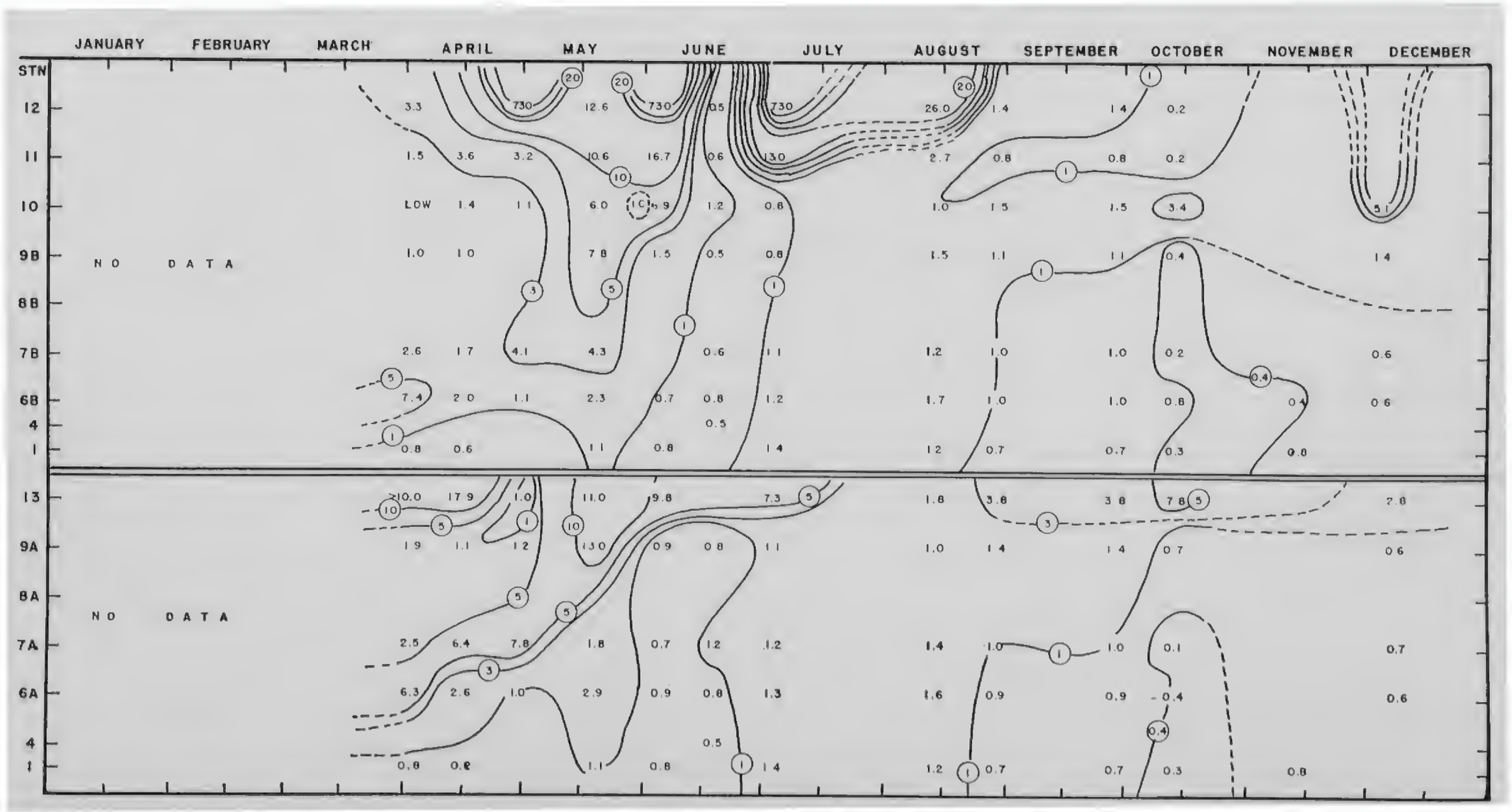


FIG. 14. The seasonal changes in nitrate in the bottom water of Great Pond in 1954, expressed in microgram atoms N/L. The two graphs shown are frequency polygons, described in detail in the legend for Figure 12.

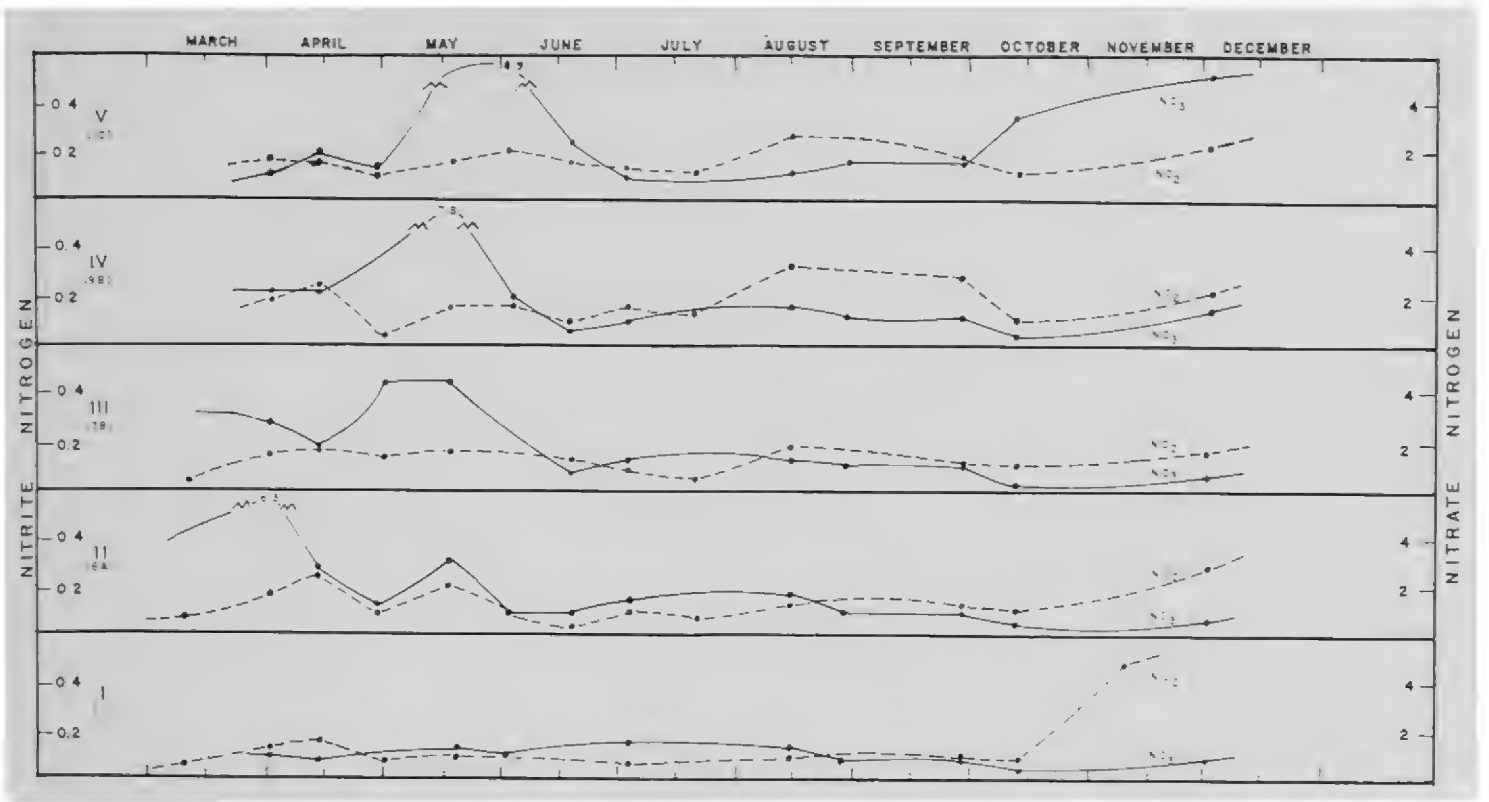


FIG. 15. Seasonal distribution of nitrite (NO_2) and nitrate (NO_3) in the bottom water of Great Pond by hydrographic sections (Figure 2) in 1954, expressed in microgram atoms N/L.

Table 4) mentioned earlier. All these responses may have been related to a nitrogen deficiency.

The seasonal changes in the phosphorus content for Great Pond are given in Figures 13, 17, 18, 19. The relatively low concentrations in spring and fall with possible limiting amounts of phosphorus in April and June suggest phosphorus as well as nitrogen may have limited growth in Great Pond.

Phosphorus concentrations are charted in Figures 17, 18, and 19. Diminished growth of benthic vegetation may be observed in Figures 4, 5, 6; Tables 4, 5. Species present in the spring first appeared in March, sustained diminished growth rates in April, but increased again in May. In April PO^4-P levels were less than 0.3 μg-at. P L in the bottom water of the usually productive sections of the estuary (Fig. 2, sections II–IV). Another period of reduced standing crops for many of these and some additional species occurred in June. At this same time PO^4-P concentrations had decreased to low values. Not all species in the estuary were equally affected by the low supply of nutrient salts. Different species have different minimum nutrient requirements (see review by Ketchum, 1954). Unfortunately, there are few published data on the minimum nutrient requirements of attached marine plants (Feldmann, 1951).

During the winter months in 1952–53, when nutrient salts were in highest concentration, the six species of *Vaucheria* found in Great Pond marshes were in fruit (Table 2). When these species were still showing good vegetative growth in late summer to fall, nutrients were possibly near limiting levels. Whether the nutrient cycles in the marsh areas are similar to those in the basin is not known.

The largest supply of inorganic phosphate and nitrate (Figs. 13 through 19) occurred in the estuary within hydrographic sections II and IV (Fig. 2). These sections were also the scene of the highest plant production per unit area in the entire estuary (Fig. 9, Table 2). The sea grasses, *Ruppia maritima* and *Zostera marina* (Fig. 7), which represent an important part of the plant biomass in summer, are most abundant in these sections of the major basin of Great Pond. Since sections II and IV were the scene of marked tidal water exchanges (see current velocities, Fig. 20), more nutrients per unit

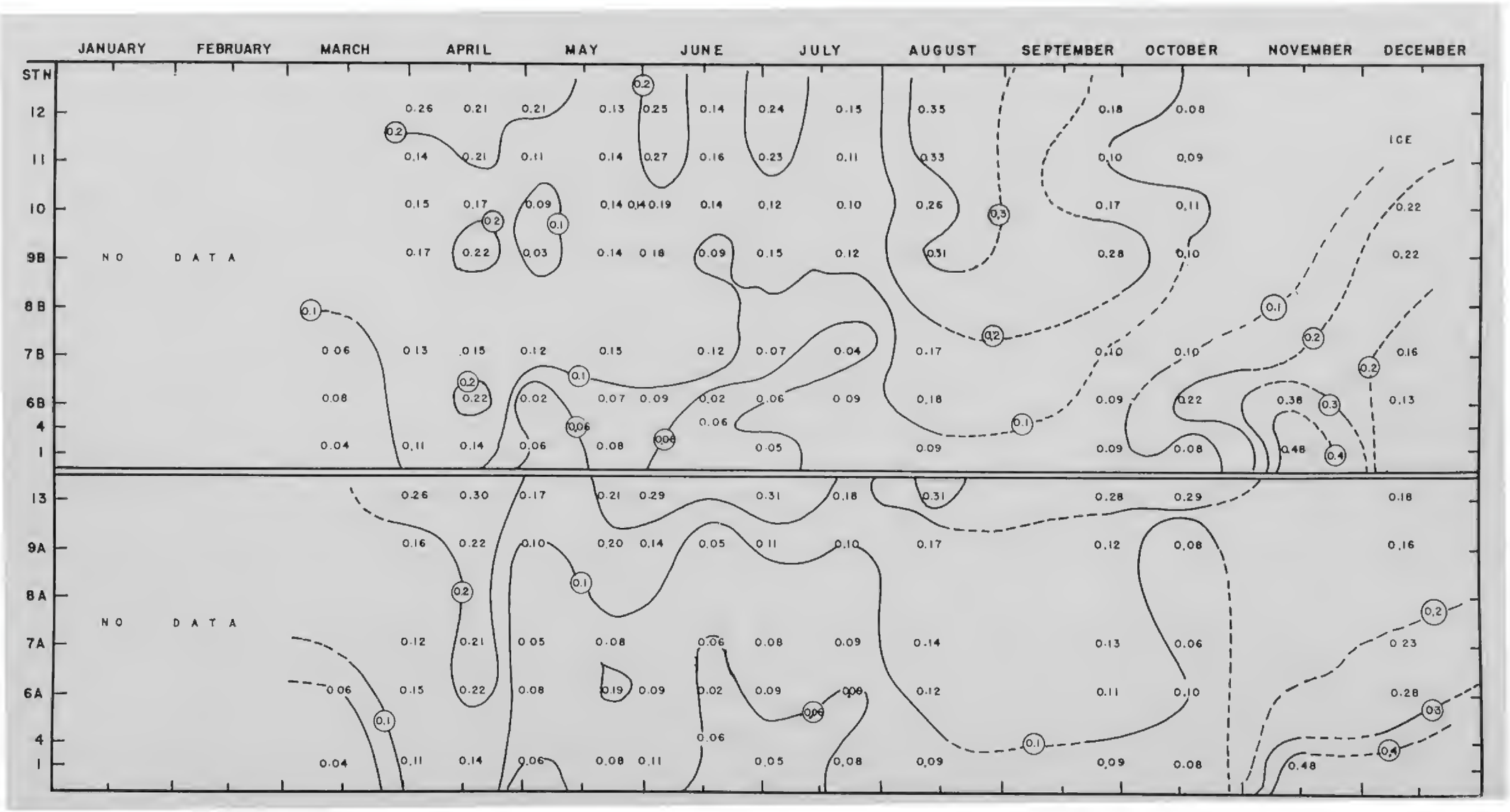


FIG. 16. The seasonal changes in nitrite in the bottom water of Great Pond in 1954, expressed in microgram atoms N/L. The two graphs are frequency polygons, described in detail in the legend for Figure 12.

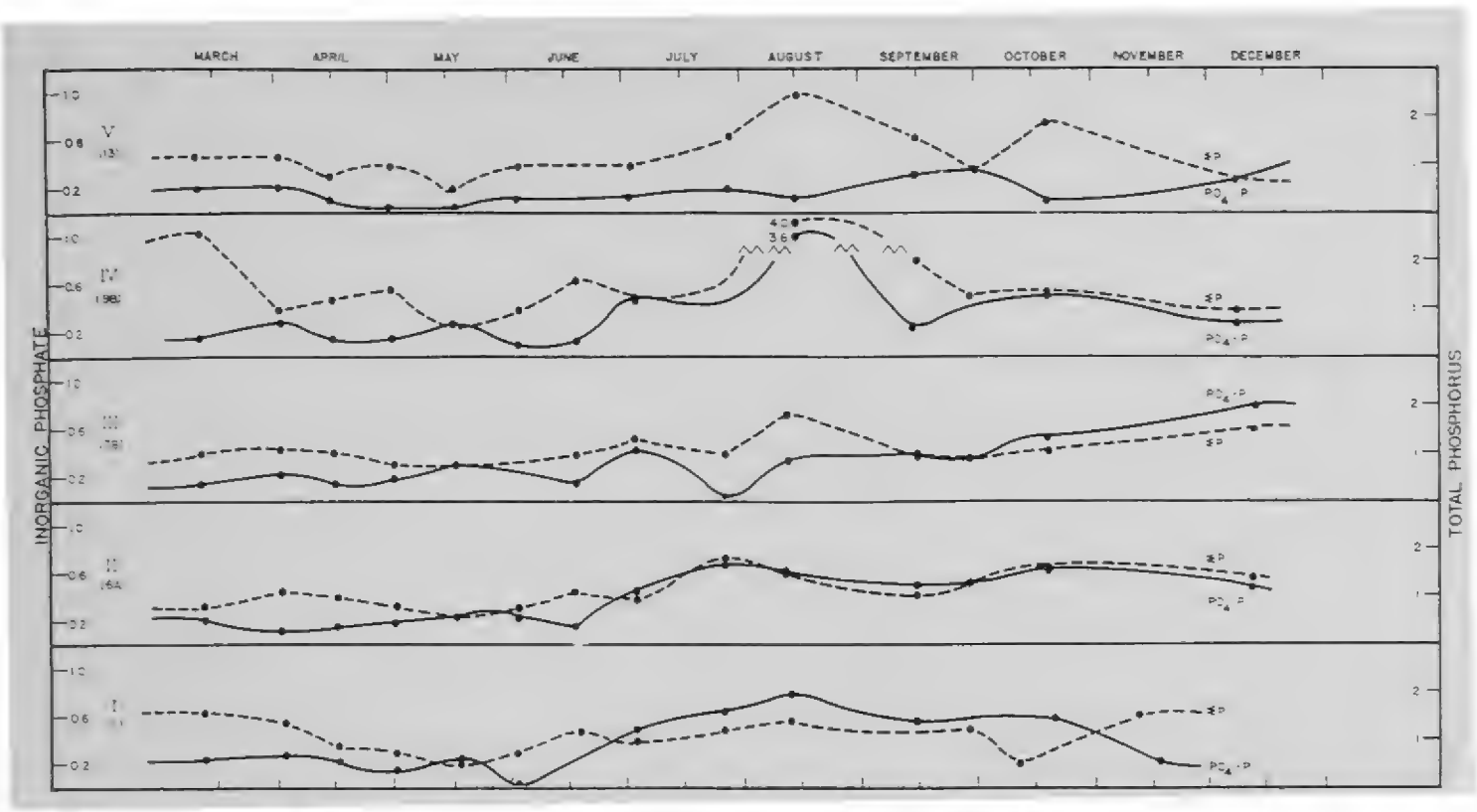


FIG. 17. Seasonal distribution of inorganic phosphate (PO_4–P) and total phosphorus (ΣP) in the bottom water by hydrographic sections (Figure 2) in Great Pond in 1954, expressed in microgram atoms P/L.

of time due to currents may have aided plant production in these areas (Gessner, 1952).

Thus the recycling of organic materials in Great Pond may occur primarily *in situ* possibly augmented by contributions from Vineyard Sound and terrestrial run-off. Hulburt (1956) did not include macroscopic benethic plants in his explanations for seasonal phosphorus changes in Great Pond. The nutrient limitations may help to explain why plant growth in Great Pond is limited and irregular.

Dissolved Oxygen and Growth

The effects of oxygen deficiency on benthic plant growth could not be observed in Great Pond since no anaerobic conditions were observed in the bottom water at any season. Oxygen data for 1952–53 and 1954 (Figs. 13, 21, 22) substantiate this conclusion. Ketchum (personal communication) did measure an oxygen deficit 0.0 ml. O_2/L in Great Pond immediately following a heavy rain storm. Such short term depletions may not seriously affect plant growth in an estuary with good transport and mixing. Reduced oxygen in the bottom water in some seasons was correlated with high growth rates and the regeneration cycles of nutrients.

pH and Benthic Plant Growth

The pH of the bottom water (Figs. 22, 23) may have had some direct influence on benthic plant growth especially in brackish water. Maximum growth occurred in the "tidal" zone (Fig. 2) of Great Pond where there was only a limited annual range of pH between 7.8 and 8.2. pH may affect plants by controlling the carbon dioxide state available for photosynthesis. The brackish waters exhibited pH extremes from 7.0 to 8.4. During the summer months growth rates (Fig. 23) were highest (Fig. 3) during periods of lower pH (7.8 usually). One explanation is that overall attrition and respiration may have exceeded photosynthesis during peak growth periods causing the pH to drop. It is also possible that the regeneration of nutrients during such periods may have stimulated growth in particular plants.

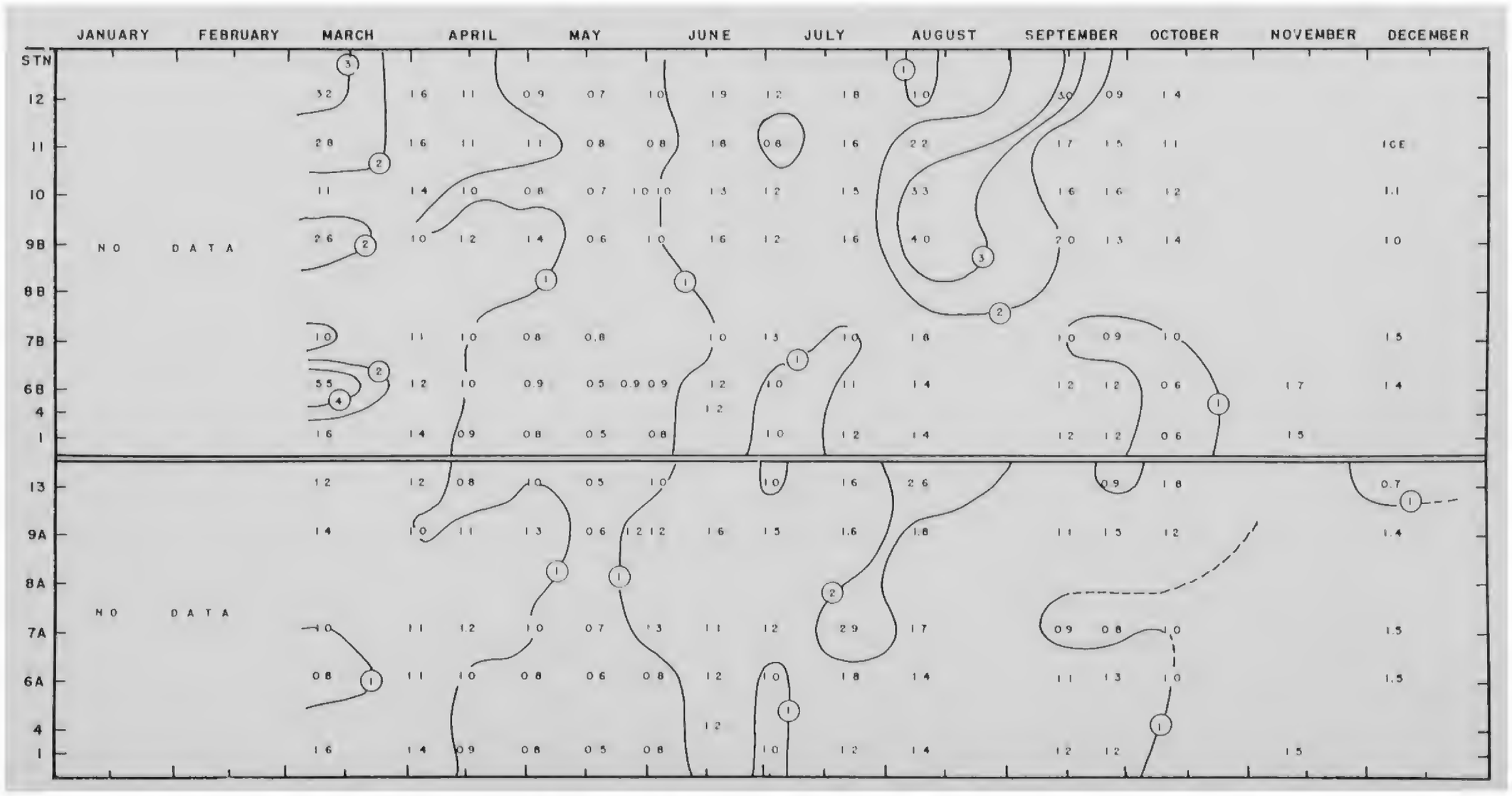


FIG. 18. The seasonal distribution of total phosphorus in the bottom water of Great Pond in 1954, expressed in microgram atoms P/L. The two graphs shown are frequency polygons, described in detail in the legend for Figure 12.

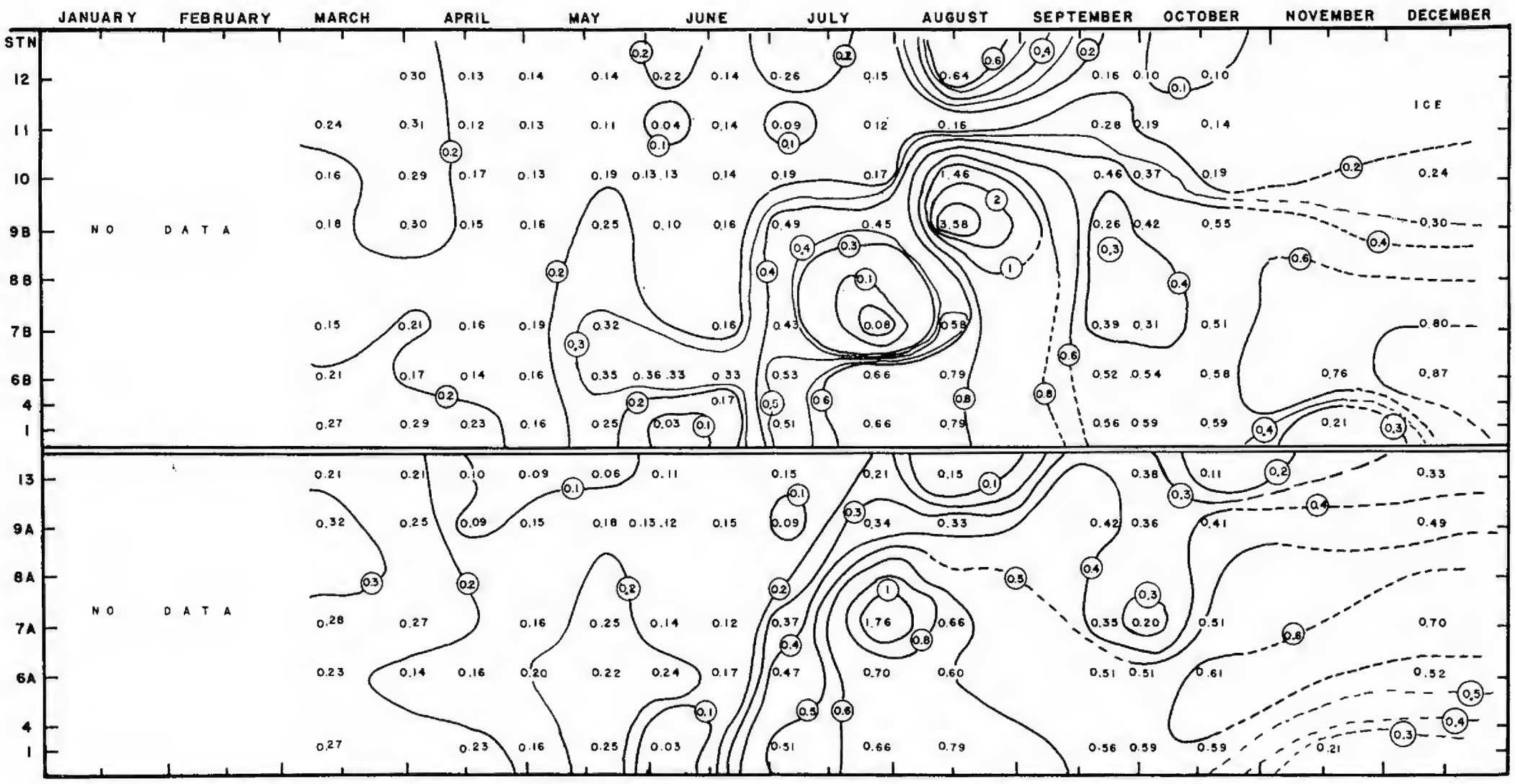


FIG. 19. The seasonal distribution of inorganic phosphate in the bottom water of Great Pond in 1954, expressed in Microgram atoms P/L. The two graphs are frequency polygons, described in detail in the legend for Figure 12.

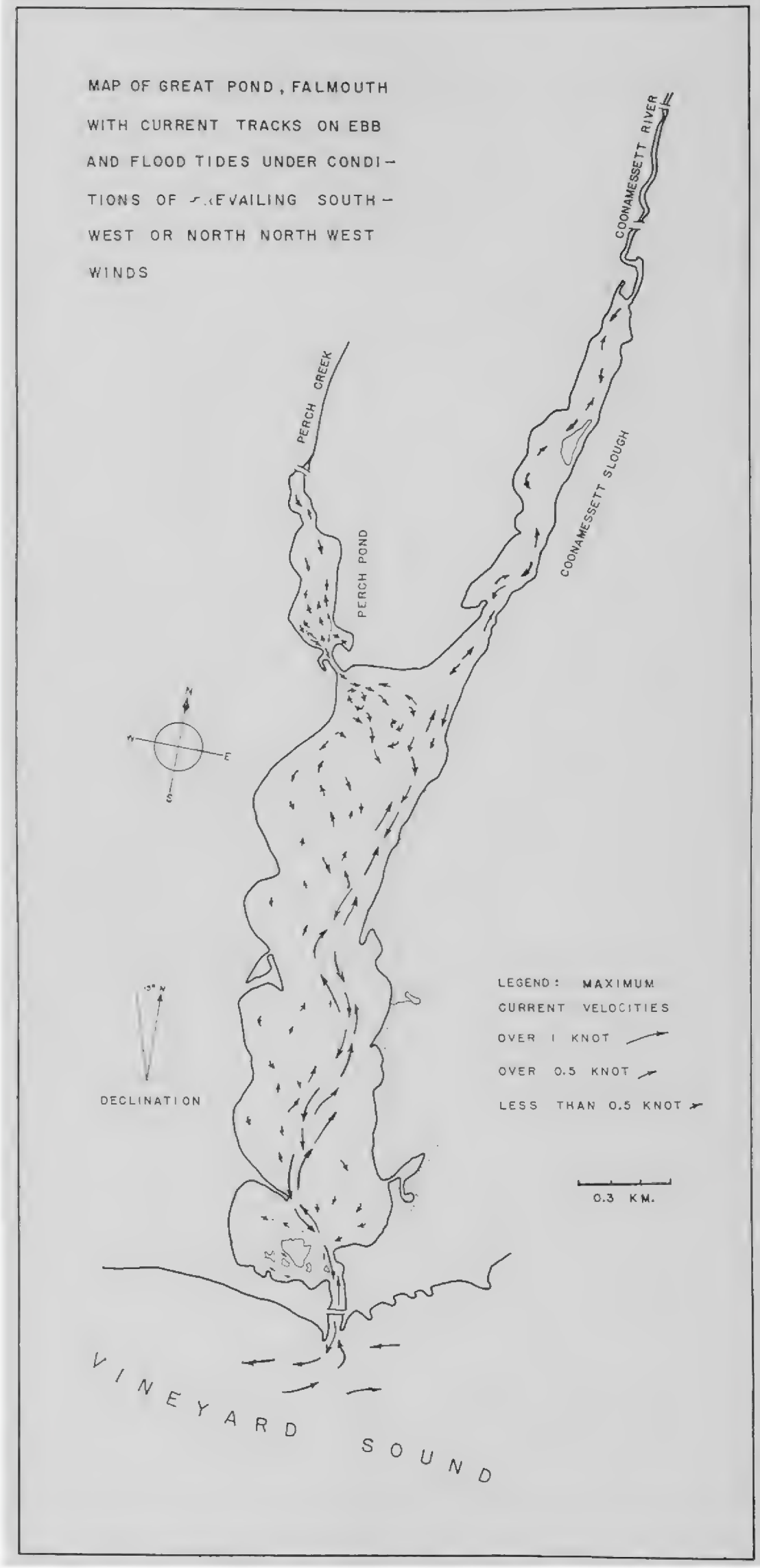


FIG. 20. Map of Great Pond, Falmouth with current tracks on ebb and flood tides under conditions of prevailing southwest or north northwest winds. Maximum current velocities are indicated by arrows.

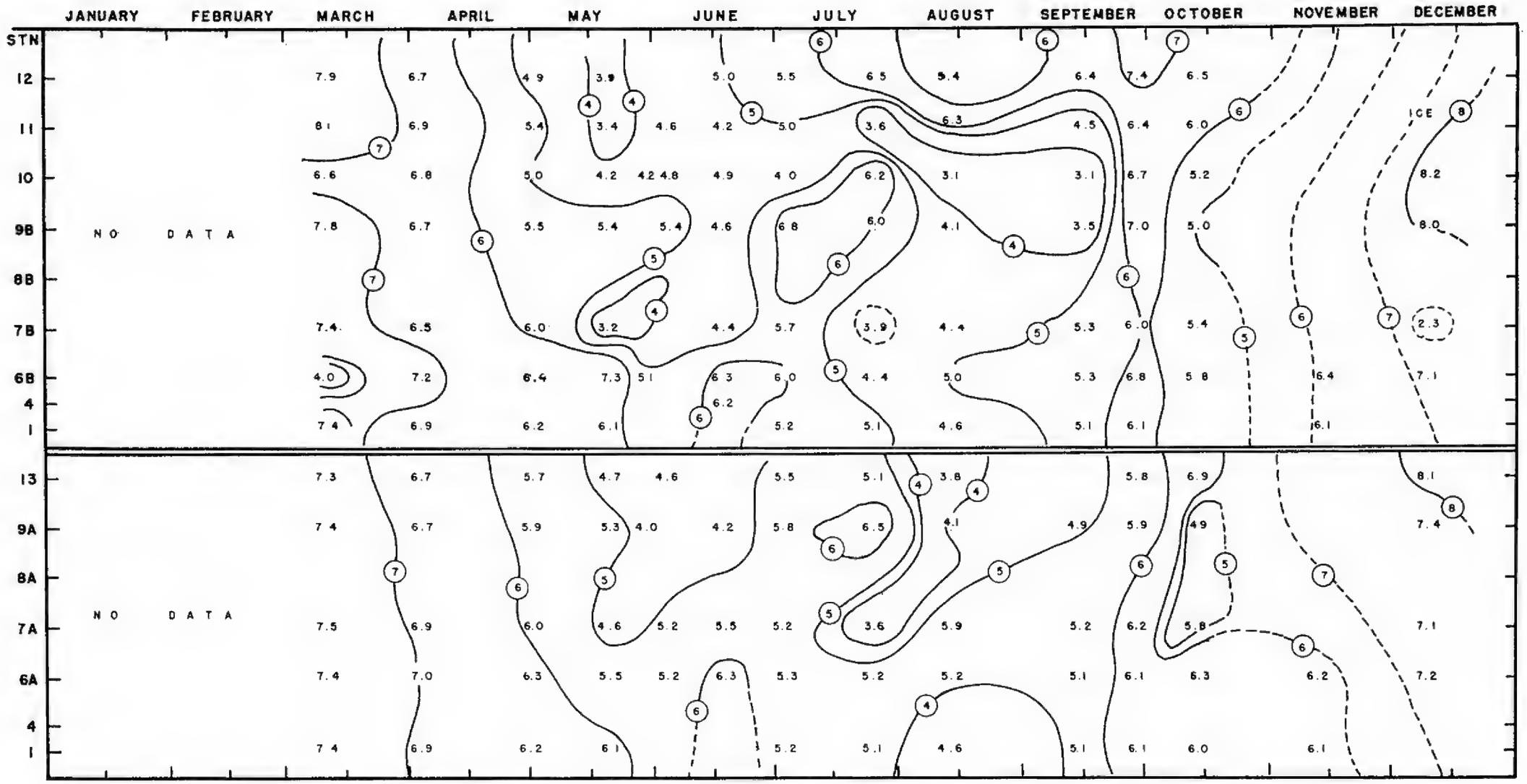


FIG. 21. The seasonal distribution of dissolved oxygen in the bottom water of Great Pond in 1954, expressed in milliliters per liter. The two graphs are frequency polygons, described in detail in the legend for Figure 12.

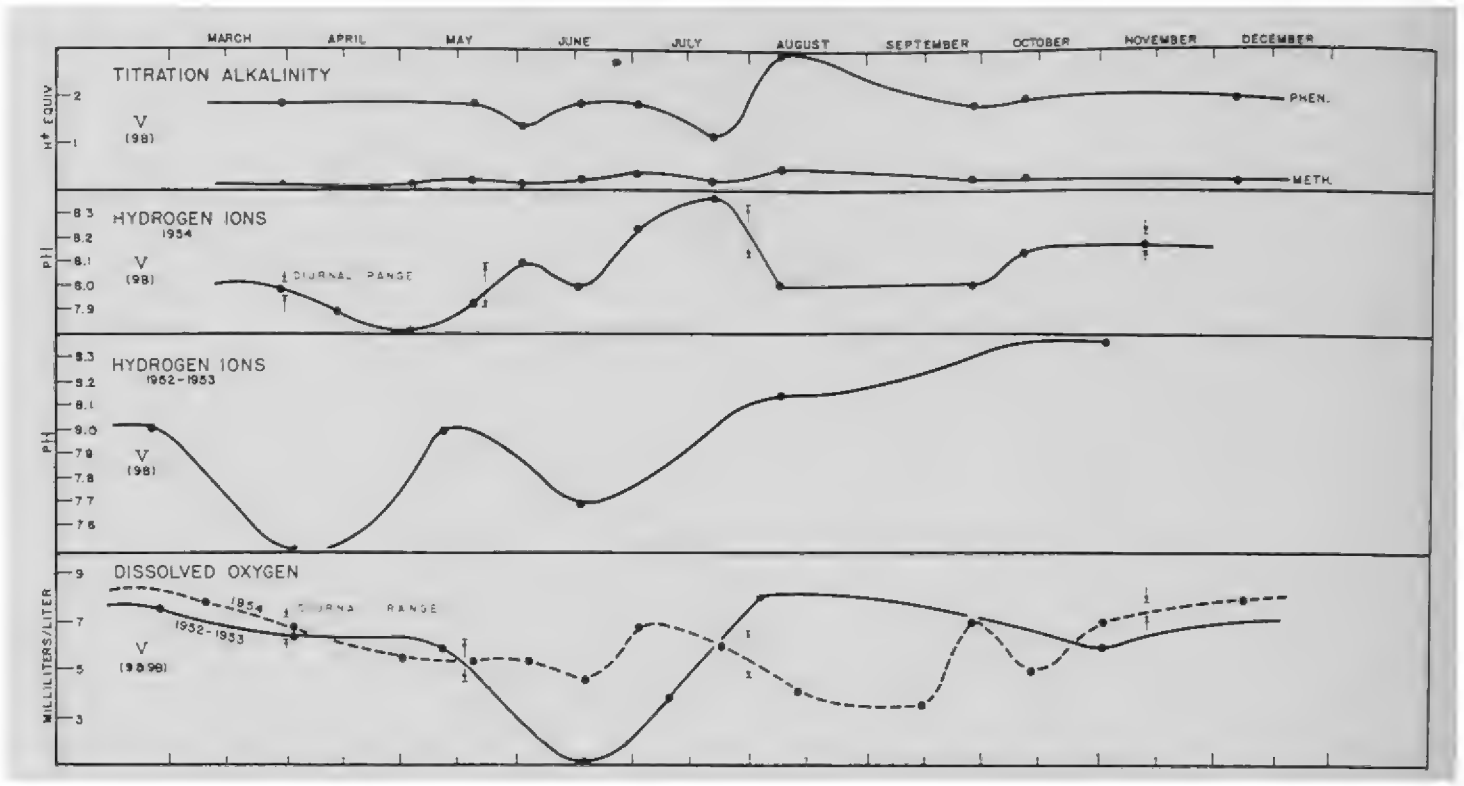


FIG. 22. Seasonal changes in titration alkalinity in 1954 and pH and dissolved oxygen in the bottom water of the "transition" zone of Great Pond in 1952–53 and 1954.

PHYSICAL FACTORS AND THE DISTRIBUTION OF BENTHIC PLANTS

Wave Action: When intense storms, occurring in the period from October through December, sweep over the estuary, waves have been observed to reach the bottom and to leave ripple marks. Poorly anchored benthic plants such as *Agardhiella tenera, Gracilaria verrucosa* and *Stilophora rhizoides* were transported a considerable distance as observed on several occasions. The occurrence of severe northeasterly storms has probably been largely responsible for the dense accumulation of algal beds within the arcs of the sand spits of the western shore. These arcs are also the scene of substantial changes in sedimentation during such storms.

The net movement of the poorly anchored species is mostly across the long axis of the estuary. Especially after a period of high winds, moribund plants of *Gracilaria* and *Agardhiella* were found in the sloughs. These plants, which presumably came from the major basin, differed from those which normally grow in the sloughs. Slough inhabiting plants have distinct modifications, such as short internodes and bushy habits.

Storms frequently separate the dying elements in the plant communities of the basin and collect them into windrows on the beach. This action tends to provide space for the younger, healthier plants in the habitat and at the same time aids in the recycling of nutrient salts.

Current: Paths taken by the flooding and ebbing tidal currents in Great Pond pass over areas abundantly populated by attached juvenile plants and by more fully developed algae attached to cobble. In Figure 24 are shown small areas where deposits of coarse sand cobble coincide with the tracks of tidal current (Fig. 20) near shore, and in narrow channels. Three explanations are offered for the abundance of the plants in the areas with currents. Active tidal currents probably transport a large number of viable spores over these areas from both neritic water and the estuary. Second, due to the constant movement of tidal water, more nutrient salts per unit of time are probably supplied to the plants in the path of the currents (Odum and Hoskin, 1957). Third, coarse sediments for attachment generally are present where water movements are

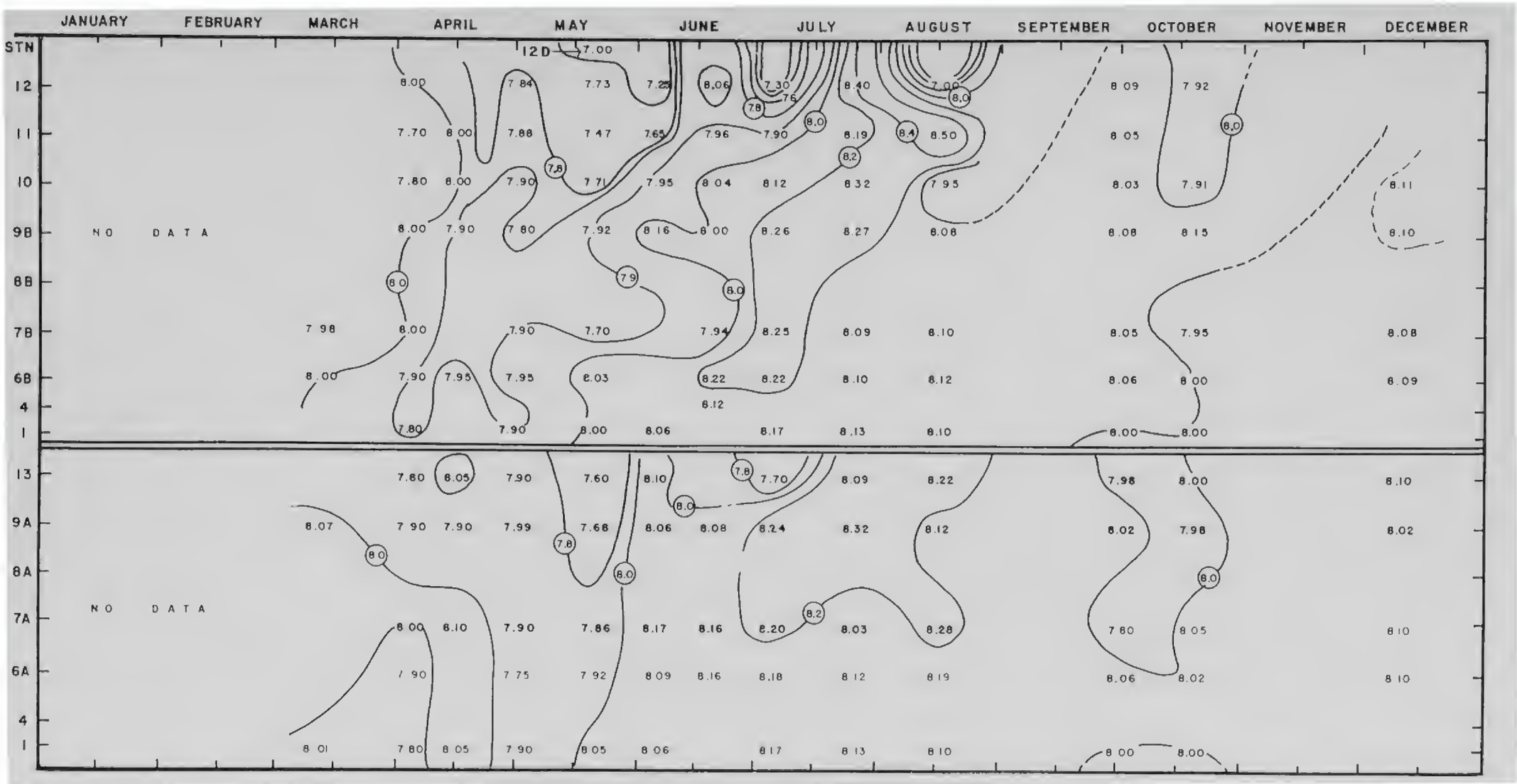


FIG. 23. The seasonal distribution of the pH of the bottom water of Great Pond in 1954. The two graphs are frequency polygons described in detail in the legend for Figure 12.

rapid. Such coarse sediments in Great Pond include large sand grains, pebble, cobble and boulder. These coarse materials probably were deposited by glacial outwash streams and are being eroded from the shoreline of the estuary. They are now very suitable for plant attachment.

Sedimentation: Butcher's data (Fig. 24) provide evidence for the development of sandy slopes strewn with pebble and shell on both shores, whereas the bottom is silt-covered. There is believed to be a correlation between the abundance of juvenile plants on the sandy shoals of the shoreline and the poorly anchored, well developed plants found on the basin floor. Poorly anchored, well developed plants growing in the major basin were nearly always attached to a sizeable sand grain, pebble or shell fragment. The cycle of events suggested by these findings starts with the attachment of spores and growth of juvenile plants on the coarse sediments of the sandy shoals. As these plants grow to some height, they are transported by wave action into deeper water where they accumulate in large masses. Eventually the algae die, after one or more seasons, and are cast upon the beach by wave action to decay. The decomposed plant debris releases nutrients for new growth. There is little doubt that this mechanism is quite necessary for the development of large accumulations of benthic plants on the basin floor.

Poor conditions for attachment, and rapid burial, are often brought on by the sedimentation of fine-grained materials in a "gradient" zone (Rochford, 1952). The fine silt enters the system in the run-off water, becomes flocculated by an electrolytic process and settles rapidly to the bottom of the sloughs. The rate of deposition is usually determined by the amount of salt present (Rochford, 1952). The soft, yielding sediments of the two sloughs (Fig. 24) are incapable of supporting attached plants. Thus, the survival of benthic plants on the slough bottom is improbable due to lack of a stable substratum. This is one reason that the floors of the two sloughs remain essentially barren of benthic plant life. Only the immediate banks and sandy shoreline slopes of the sloughs support attached algae and *Ruppia* beds.

Salinity: The effects of salinity on plants are variously related to other variables in a tidal estuary. Local distribution in estuarine water may be controlled by salinity and temperature (Luther 1951a, 1951b; Doty and Newhouse, 1954). Large changes in salinity require rather severe osmotic regulation in an organism (Sverdrup *et al.*, 1942). Certain benthic marine plants such as *Chondrus crispus, Corallina officinalis, Gelidium crinale, Nemalion multifidum, Petalonia fascia, Polysiphonia novae-angliae, Punctaria plantaginea, Ulva lactuca* var. *rigida* and others were never observed within the "tidal" or "gradient" zones of Great Pond (Figs. 2, 25) but established themselves only on the riprap along the open coast. In contrast, *Agardhiella tenera, Ectocarpus confervoides, E. siliculosus, Gracilaria verrucosa, Polysiphonia denudata, Porphyra leucosticia, Punctaria latifolia, Scytosiphon lomentaria, Spyridia filamentosa, Stilophora rhizoides* and others (Table 2) established themselves in the major basin of Great Pond and a few plants grew in the brackish water of the sloughs. In the colder months species including *Ectocarpus siliculosus, Punctaria latifolia* and *Stilophora rhizoides* were found in brackish water areas from which they were conspicuously absent in the spring. These plants were much less tolerant of low salinities at the relatively high water temperatures obtained in mid to late spring. Doty and Newhouse (1954) reported similar plant distributions in low salinity water when comparing summer and fall periods in the Oyster River. Due to a relatively uniform rainfall the year around (Table 10) seasonal (Fig.

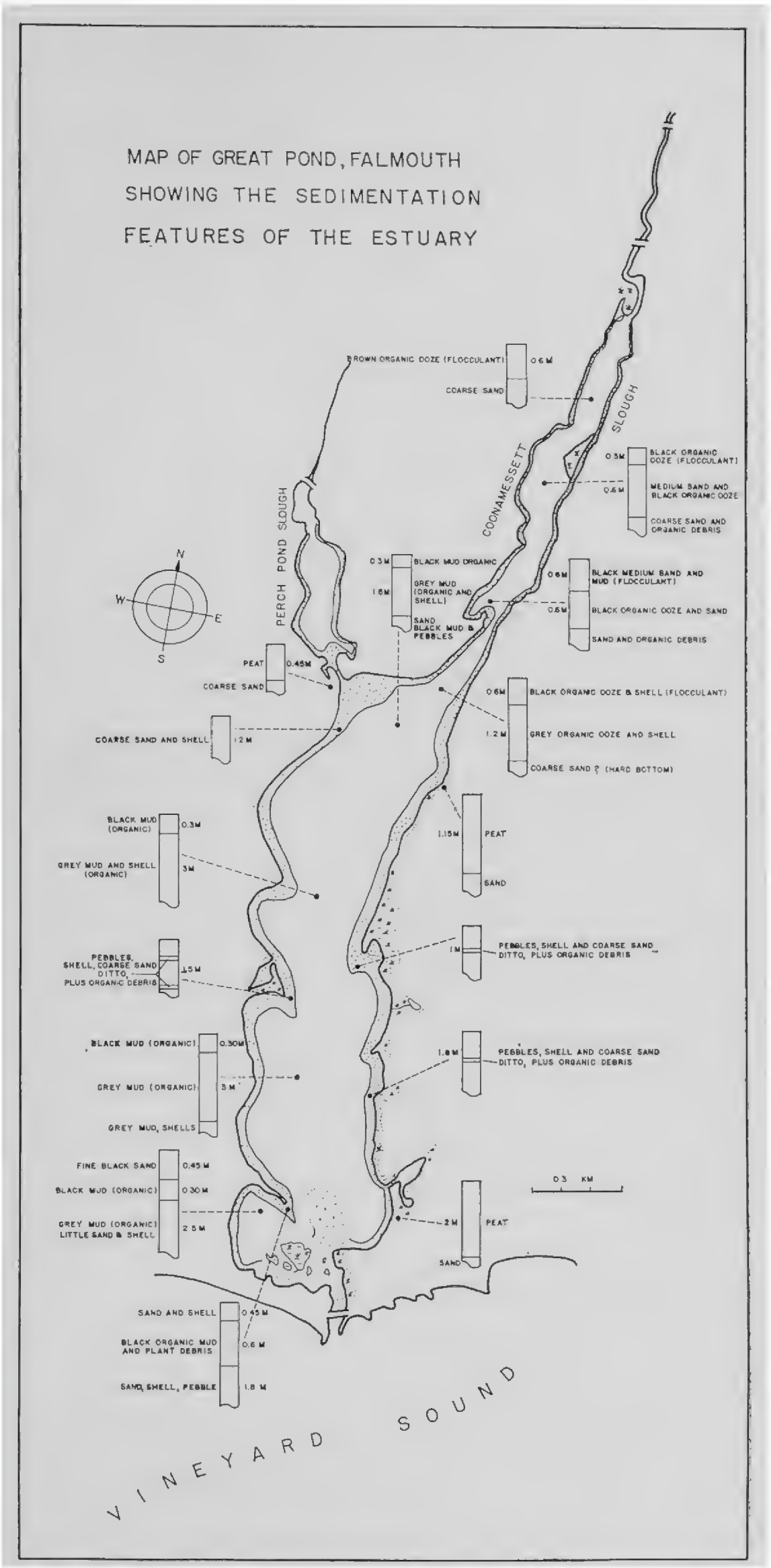

MAP OF GREAT POND, FALMOUTH
SHOWING THE SEDIMENTATION
FEATURES OF THE ESTUARY
PERCH POND SLOUGH
COONAMESSETT SLOUGH
N
W
E
S
BROWN ORGANIC OOZE (FLOCCULANT) 0.6 M
COARSE SAND
0.3M BLACK ORGANIC OOZE (FLOCCULANT)
0.6M MEDIUM SAND AND BLACK ORGANIC OOZE
COARSE SAND AND ORGANIC DEBRIS
0.3M BLACK MUD ORGANIC
1.6M GREY MUD (ORGANIC AND SHELL)
SAND BLACK MUD & PEBBLES
0.6M BLACK MEDIUM SAND AND MUD (FLOCCULANT)
0.6M BLACK ORGANIC OOZE AND SAND
SAND AND ORGANIC DEBRIS
PEAT 0.45M
COARSE SAND
COARSE SAND AND SHELL 1.2M
0.6M BLACK ORGANIC OOZE & SHELL (FLOCCULANT)
1.2M GREY ORGANIC OOZE AND SHELL
COARSE SAND ? (HARD BOTTOM)
BLACK MUD (ORGANIC) 0.3M
GREY MUD AND SHELL (ORGANIC) 3M
1.15M PEAT
SAND
PEBBLES, SHELL, COARSE SAND DITTO, PLUS ORGANIC DEBRIS 1.5M
1M PEBBLES, SHELL AND COARSE SAND DITTO, PLUS ORGANIC DEBRIS
BLACK MUD (ORGANIC) 0.50M
GREY MUD (ORGANIC) 3M
GREY MUD, SHELLS
1.8M PEBBLES, SHELL AND COARSE SAND DITTO, PLUS ORGANIC DEBRIS
FINE BLACK SAND 0.45 M
BLACK MUD (ORGANIC) 0.30 M
GREY MUD (ORGANIC) LITTLE SAND & SHELL 2.5 M
0 .3 KM
2M PEAT
SAND
SAND AND SHELL 0.45 M
BLACK ORGANIC MUD AND PLANT DEBRIS 0.6 M
SAND, SHELL, PEBBLE 1.8 M
VINEYARD SOUND

FIG. 24. Map of sediments of Great Pond based on unpublished data by Butcher.

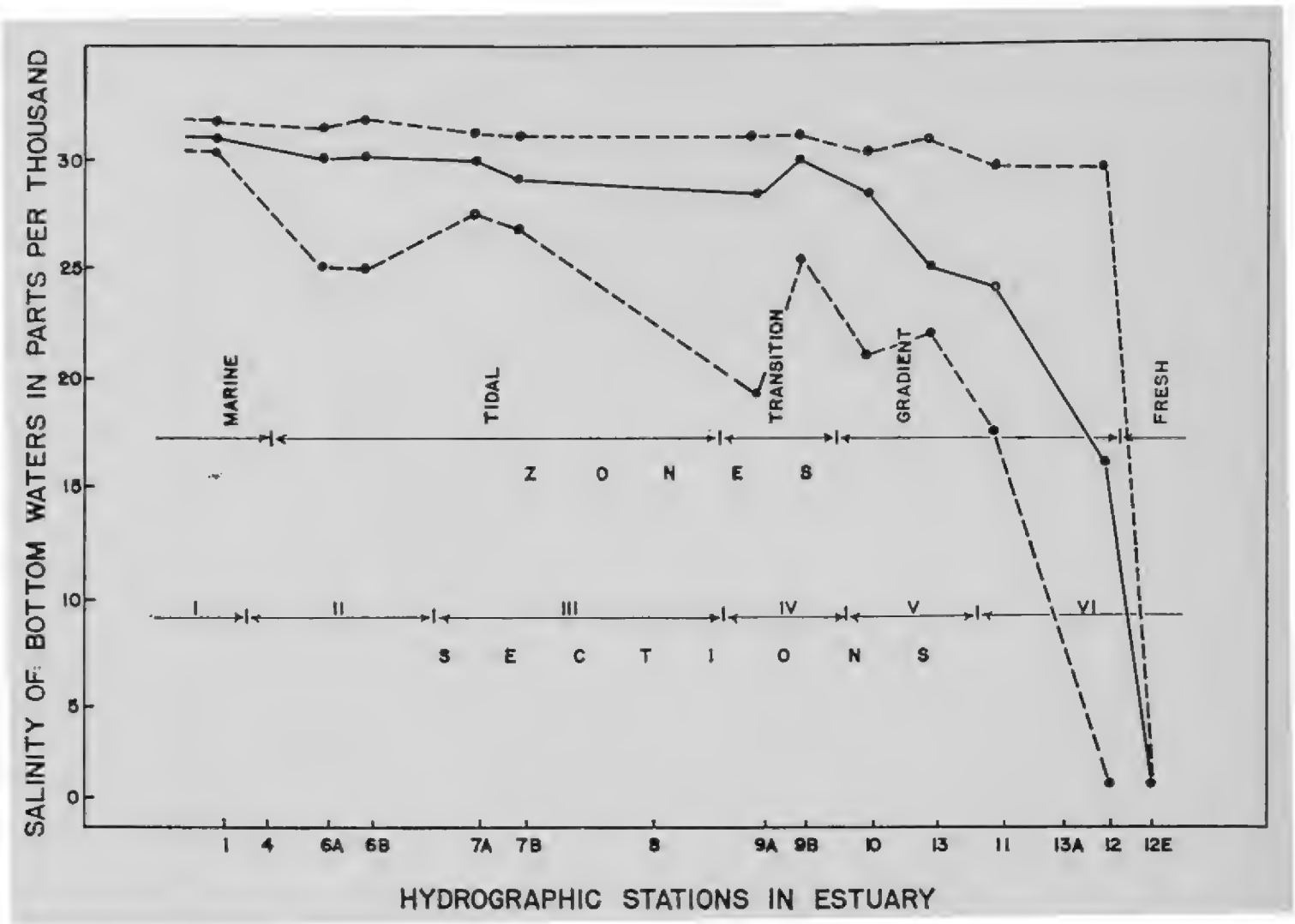


FIG. 25. The annual means and extremes of salinity of bottom water in Great Pond, Falmouth along the long axis of the estuary in 1952–53. Data are given in parts per thousand (0/00). The zones (after Rochford, 1952) and sections are those indicated in Figure 2. The anomalous extremes of decreased salinity at stations 6A and 6B are due to mixing of bottom water with surface water over a shoal sand bar at the seaward end of the basin (see Fig. 2).

TABLE 10

Monthly Precipitation in Centimeters for Nantucket Island, Massachusetts

	1952	1953	1954
January	16.0	20.9	13.0
February	20.5	13.7	6.0
March	11.6	15.8	6.7
April	6.6	21.4	9.8
May	8.2	4.7	9.2
June	1.7	0.5	1.8
July	0.4	14.9	2.9
August	14.9	8.0	12.2
September	1.9	11.5	12.7
October	5.1	11.1	3.3
November	5.2	19.9	11.4
December	12.1	10.0	16.2
Annual	104.2	152.4	105.2

26) and daily ranges (Barlow, 1956) in salinity were nearly the same in Great Pond. Temperatures (Fig. 12), however, varied widely with the season.

Where the dilution of sea water becomes too great, the normal growth of a species may not continue (Legendre, 1921). The sloughs are the last outpost for a few invading marine species of benthic algae and marine phanerogams and there is only a small total plant standing crop at all seasons (Fig. 7, Table 2). Considerable growths of *Enteromorpha clathrata, E. compressa, E. intestinalis, Monostroma oxyspermum* and *Ulva lactuca* var. *latissima* were found, but the two species *Enteromorpha linza* and *E. minima,*

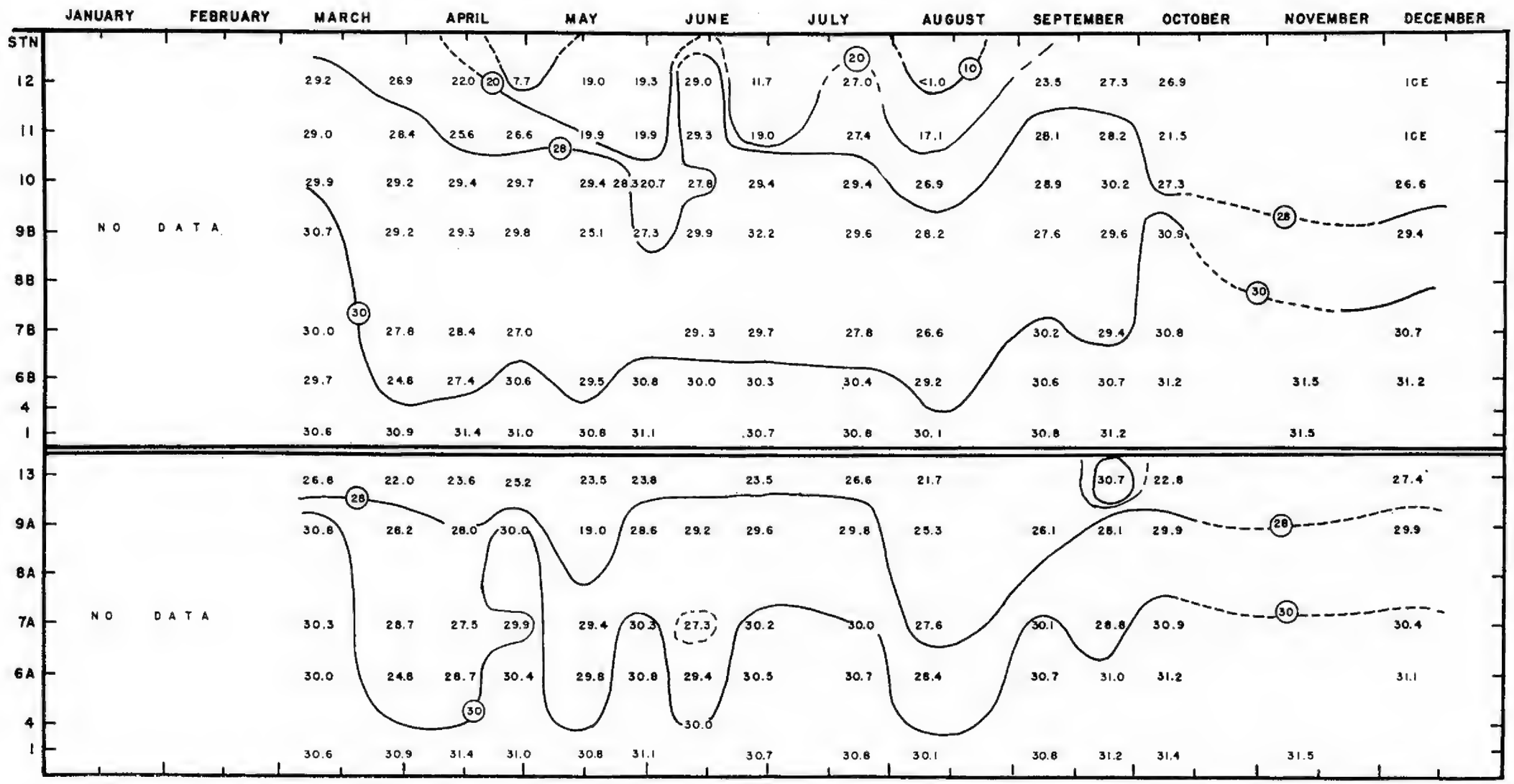


FIG. 26. The seasonal patterns of salinity in parts per thousand in the bottom water of Great Pond in 1954. For explanation of the coordinates see legend of Figure 12.

were never found in brackish water. Reduced salinities were characteristic of the "transition" zone (Figs. 25, 26; Table 2) yet the area supported a large portion of the total plant material in the estuary. Brackish water in the sloughs apparently greatly reduced growth and caused abnormal ties in some species of marine plants such as *Ceramium rubrum, Gracilaria verrucosa, Punctaria latifolia, Scytosiphon lomentaria* and *Spyridia filamentosa.*

There is evidence that some species of benthic marine plants remain sterile if they inhabit brackish water (Levring, 1940; Hayren, 1940, and others). In those sections of Great Pond where the mean salinity of the bottom water was below 26‰, sterility was common among the benthic algae. Probably the spores which arise on attached plants in brackish water come from plants in normal sea water habitats. Among the Phaeophyto no unilocular reproductive organs were observed in *Punctaria latifolia* or *Scytosiphon lomentaria.* The alga *Ectocarpus siliculosus,* appeared to be one of the few species in the division Phaeophyta which bore both unilocular and plurilocular reproductive structures in brackish water habitats. Nothing is known concerning the viability of the spores which this species produces in low salinity water.

The identity of specimens of *Ectocarpus siliculosus* found in the "gradient" zone may be open to question. The gametangia were more attenuated and elongated than in the typical form. Although plants of *Agardhiella tenera, Ceramium rubrum* var. *proliferum* and *Gracilaria verrucosa* grew in the "transition" and "gradient" zones (Figs. 2, 26), all specimens examined were sterile. The species, *Stilophora rhizoides,* could be separated into two morphological types in the "tidal" and "transitional" zones and the "gradient" zone respectively. The latter was smaller and finer branched. Both forms were induced to liberate swarmers in the laboratory suggesting that the species is capable of reproducing in brackish water.

Fruiting periodicity was studied in six species of marine *Vaucheria* (Blum and Conover, 1953). Fruiting occurred in several species from January through May soon after the occurrence of spring tides. Thus fruiting appeared to be related to prolonged immersion in water of much higher salinity than normal for the habitat.

Water Density: Whereas there seemed to be no clear-cut correlation between temperature or salinity alone and the seasonal occurrence of some benthic marine plants, there was a correlation between density and plant growth. Some plant species grew in brackish water habitats in winter but were absent from these areas by midspring and summer. Species which followed such a pattern included *Ectocarpus siliculosus, Gracilaria verrucosa* (Figs. 5, 6), *Punctaria latifolia, Scytosiphon lomentaria* and *Stilophora rhizoides* (Figs. 4, 6). These plants grew in brackish water as long as the water density (Fig. 27) was above 20 sigma-t units (1.020 gm./cc.), but disappeared from the sloughs when the density fell below 20 sigma-t units. In the major basin, where growth was not affected, the density ranged from 20.6 in winter to 24.5 sigma-t units in summer. In the sloughs the density ranged over the year from 12.0 in summer to 22.5 simga-t units in winter. From these results it would seem that density is correlated with growth in some seasons more than either temperature or salinity alone. Exactly why there is a correlation of density and growth is not known. Boyle and Doty (1949) believed that tolerances of marine algae to diluted sea water may decrease with increases in temperature. Since density is a function of temperature and salinity, the apparent correlation may be a matter of tolerance to low salinities at low temperatures.

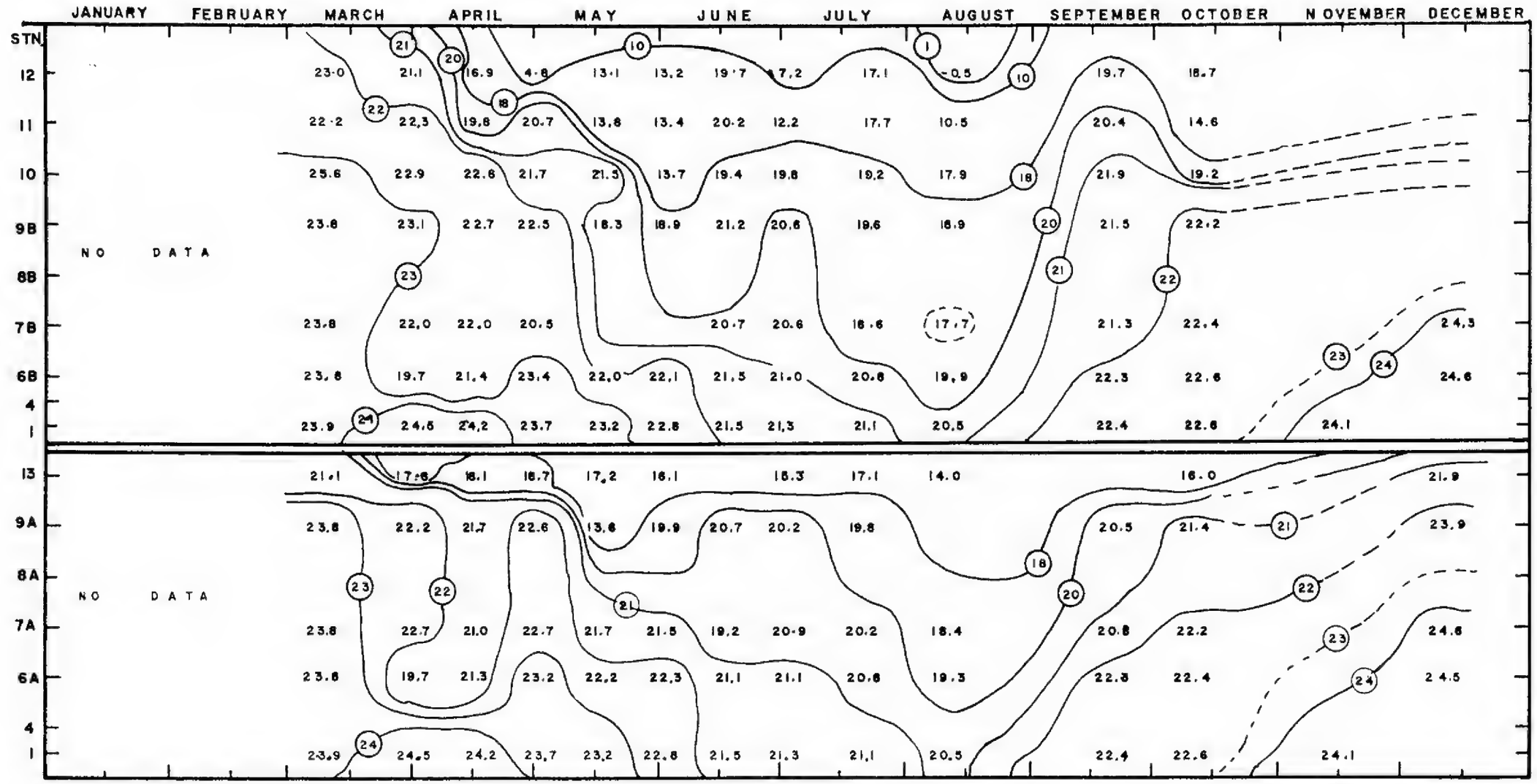


FIG. 27. Water density in sigma-t units in bottom water of Great Pond in 1954. The two graphs shown are frequency polygons, described in detail in the legend for Figure 12.

Biotic Factors and Seasonal Growth

Animal grazing apparently begins or takes place immediately after there is an initiation of phytoplankton growth (H. W. Harvey, 1955). With benthic marine plants in Great Pond, there is a period in early growth when grazing and epiphytism appear to be slight.

Immature plants of *Agardhiella tenera, Ceramium rubrum, Gracilaria verrucosa* and *Polysiphonia novae-angliae* were studied periodically to observe the relationship between growth and attack by other organisms. Very little grazing by the snails, *Bittium alternatum* or *Nassa obsoleta,* was witnessed. Only slight coverage by algal epiphytes was noted. On well developed plants about three weeks old many evidences of grazing were found, and epiphytes were noticeable with the unaided eye. Epiphytism and grazing were marked when the species populations had attained or passed their peak production levels.

Summer populations under conditions of high illumination and temperature were those most severely affected, but *Polysiphonia novae-angliae* showed attack by epiphytes and grazing early in its growth period. During the time of most active growth, attached plants in normal sea water did not seem to be seriously reduced by animal grazers. Observations on some marine plant species in both normal sea water and brackish water indicated that many more epiphytes had developed, and grazing by gastropods was far more intense on plants growing in more brackish water habitats than in normal sea water. Apparently, plants, whose optimum growth processes take place in normal sea water, are less able to resist attack and predation during early growth in a brackish environment.

Although morphological differences provide adequate grounds for establishing varieties in algae, other evidence may also be used. Seasonal growth data on varieties of *Ulva lactuca* provided evidence for a separation. In Great Pond *Ulva lactuca* var. *latissima* and *Ulva lactuca* var. *rigida* (Figs. 4, 6) exhibited dissimilar seasonal growth patterns.

Storms, Extreme Temperatures and Icing

Winds and Tropical Hurricanes: During the entire 1952–53 survey period water temperatures were mild (Fig. 11) and no violent storms (Fig. 10) were recorded. Thin sheets of ice formed on the sloughs only for a brief two-week period in February. According to the small deviation from the 62-year norm for the area (Table 10) rainfall in the survey years was fairly normal except in January and April, 1953. The illumination received in the summer of 1952 was somewhat above average. Measurements of standing crops of the dominant benthic marine plants during 1952–53 were believed to be representative for tidal estuaries on the Cape, according to sample surveys of several other estuaries along the southern coast of the peninsula. From June 1952 to August 1954 average climatic conditions prevailed in New England.

On August 31, 1954, a tropical hurricane swept over southern New England, bringing over 180 km. per hour wind velocity and 13 cm. of rainfall to the south Cape region. This storm was followed by a second one a week later. A series of salinity measurements were made in Great Pond to observe what had taken place (Table 11). Following the first hurricane, "Carol," the salinity of waters in Vineyard Sound increased only about 1‰ at the seaward end of the major basin. Then due to the heavy rainfall accompanying

TABLE 11

Salinity in Parts per Thousand in Great Pond Before and After Hurricanes "Carol" and "Edna", September, 1954

(Figure 2) Stations	Level	July 23	Aug. 11	Aug. 31	Sept. 8	Sept. 11	Sept. 16	Sept. 27
6A	surface	30.6	27.1	Hurricane	31.0	Hurricane	30.5	31.0
	bottom	30.7	28.4	"Carol"	31.0	"Edna"	30.7	31.0
9A	surface	19.7	20.5		16.4		26.1	28.6
	bottom	29.7	25.3		30.0		26.1	28.1
10	surface	28.6	8.5		4.7		23.2	8.0
	bottom	29.4	26.9		27.0		28.9	30.1
1	surface	30.8	29.9		31.2		30.5	31.0
	bottom	30.8	30.1		31.2		30.8	31.2

the two storms, salinities decreased in the surface waters of the sloughs as the river discharge rate nearly doubled the normal amount for that season. These changes in salinity had little effect on the benthic vegetation according to a cursory examination. Precipitation in hurricanes had a greater effect on salinity than high storm tides. At any rate, such changes are quite temporary.

Wave action on the riprap disarranged the boulders, stripped most of the larger plants off the rocks and removed large amounts of the basin-inhabiting algae from Great Pond. In the summer of 1956 quadrat studies were made on transect 6 (section II, Fig. 2) to determine the fate of benthic plant populations. To all appearances the former luxuriance of the benthic vegetation had been restored.

Extreme Low Temperatures and Icing: In 1955, ice completely covered Great Pond to a depth of 7 cm. and persisted from January 20 through February 12. In 1956 icing conditions were even more severe. An ice sheet, which had a maximum thickness of 12 cm., remained for six weeks over the estuary. Inspection of the riprap at the mouth of the estuary showed ice-scouring had removed large quantities of *Chondrus crispus*, *Corallina officinalis* and *Fucus spiralis* but had done little damage to populations of *Fucus vesiculosus*. The latter occupies a sublittoral position on the riprap. Ice-scouring affected the attached plants on most Falmouth jetties during this period also, as large sheets of fringe-ice lined the shore. For the first time in nine years (records of the Woods Hole Oceanographic Institution), Buzzards Bay was covered by large sheets of ice which broke off during the thaw as large chunks passed through Woods Hole and entered Vineyard Sound.

The effect of low water temperatures and subsequent icing during this period also may have been responsible for the near extinction of *Gelidium crinale*. This species occupied a habitat in the intertidal belt where ice-scouring was severe. At this time the alga, *Bostrychia rivularis*, disappeared from section IV and could not be found anywhere in the estuary through the summer of 1956. The alga, *Punctaria plantaginea*, so abundant in the winter of 1952–53 did not appear along the Falmouth coastline in 1954 or the following winters through 1957. No explanation could be given for disappearance of a species that is found characteristically in arctic waters in a sublittoral habitat little affected by icing (Kjellman, 1883).

SIMILARITIES AND DIFFERENCES IN SUCCESSIVE YEARS

A question arises in a two-year study such as the present one in which the biotic survey was made one year and the hydrological survey the second year. Can one logically relate the biological data for 1952–53 to oceanographic data for 1954? Since some properties

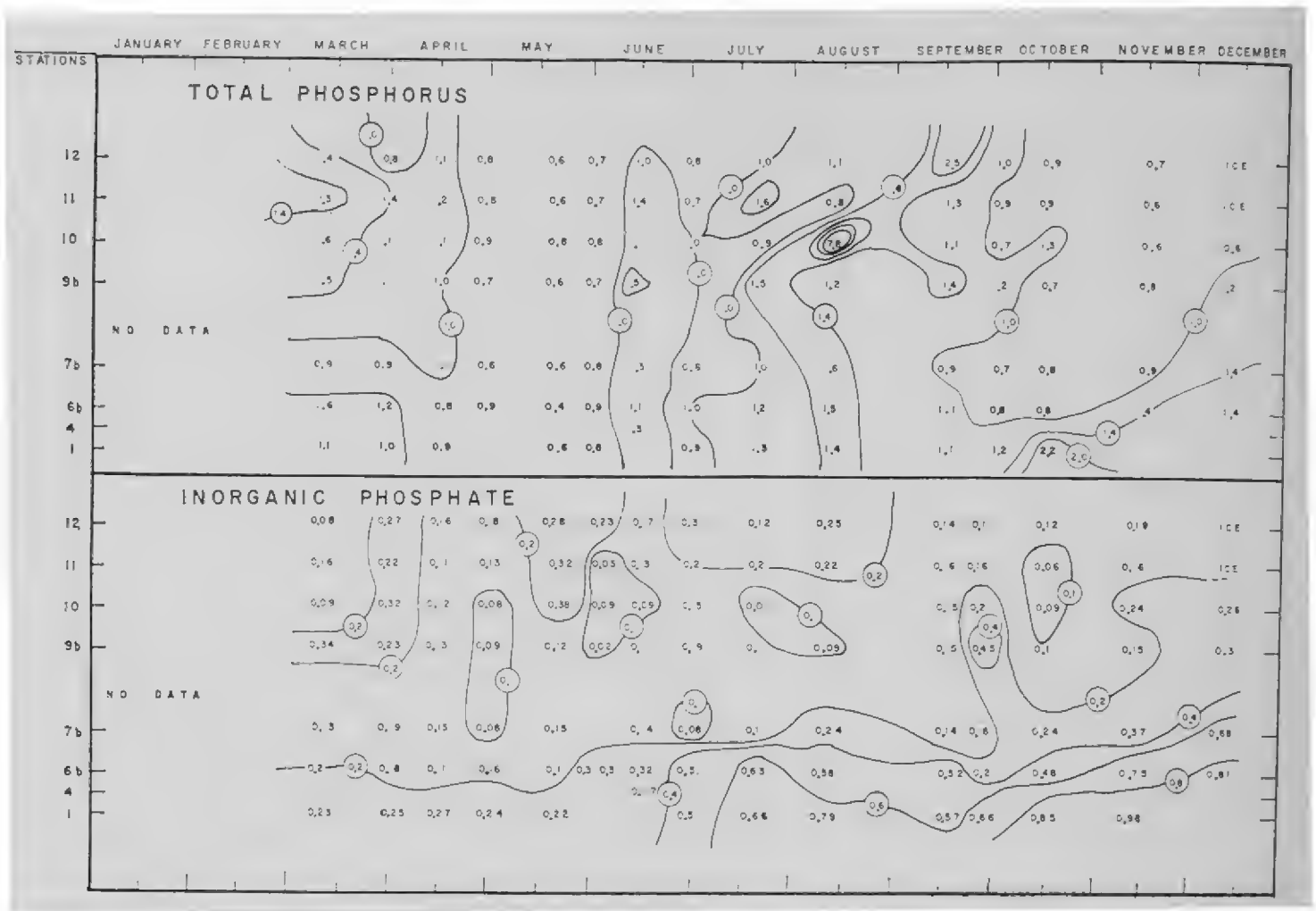


FIG. 28. Total phosphorus and inorganic phosphate in the surface water of Great Pond in 1954, expressed in microgram-atoms P/L. The two graphs shown are frequency polygons. Stations were located at the center in 1951 and along the eastern side of the pond in 1954. Refer to Figure 12.

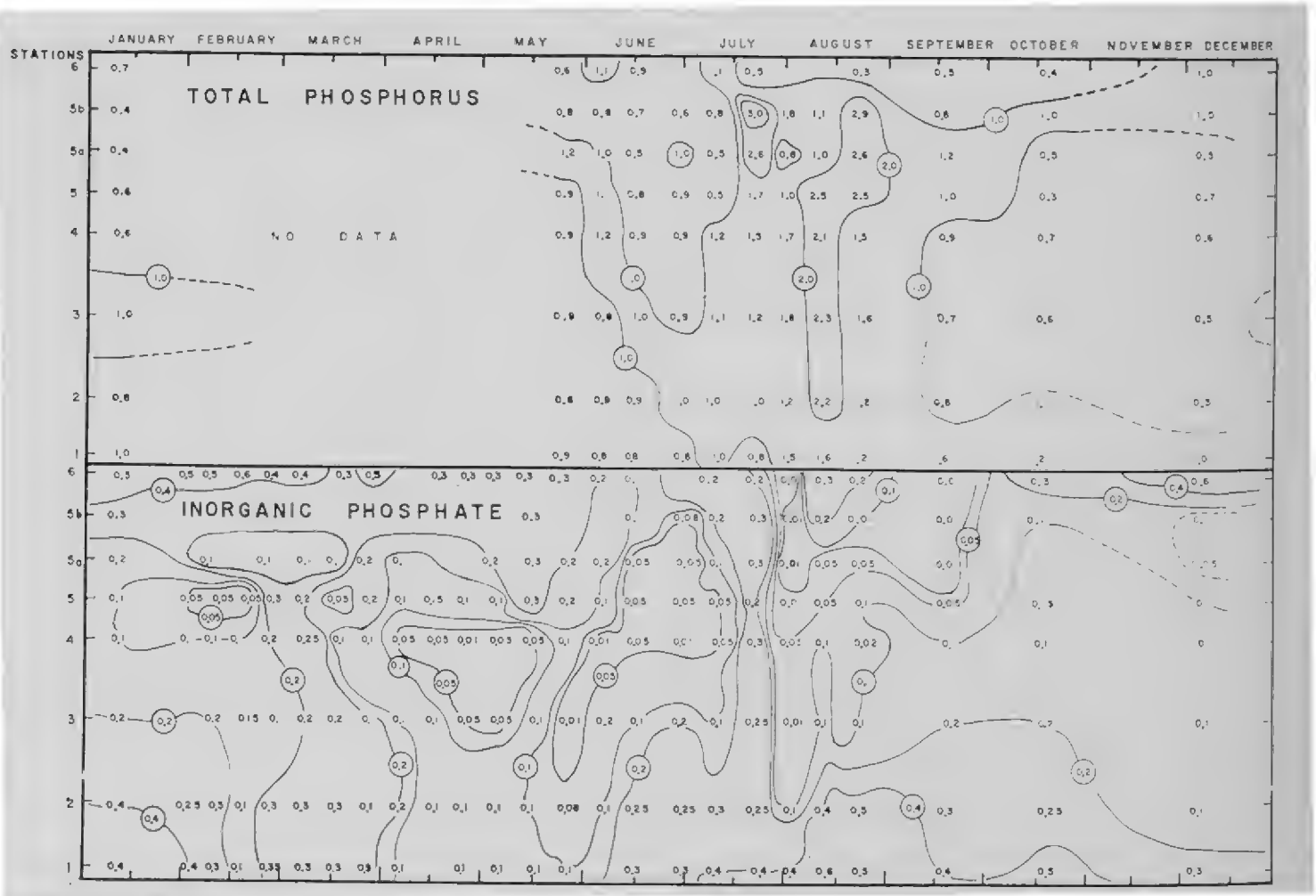


FIG. 29. Total phosphorus and inorganic phosphate in the surface water of Great Pond in 1950 (data after Hulbert), expressed in microgram atoms P/L. Compare these data with those of Figure 28 for 1954. The legend is the same as for Figure 28.

were measured in both years, a partial answer can be given. In Figure 22 dissolved oxygen and pH for 1952–53 and 1954 have been plotted. The same trends are present. There is also a close parallel between the 1950 and 1954 seasonal distribution of surface phosphorus. Data for 1950 are from Hulbert; Figures 28 and 29. Apparently the regular factors represented by the patterns of oxygen, pH, and phosphorus are repeated with similar amplitude from year to year.

The plant populations, however, are not exactly similar (See section on changes from year to year). It may be inferred that irregular factors and unusual departures are responsible for the changes in seasonal growth and reproduction of the plants from one year to the next.

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Artificially Formed Mud Balls

LOUIS S. KORNICKER, CARL H. OPPENHEIMER, AND JOHN T. CONOVER

Institute of Marine Science
The University of Texas
Port Aransas, Texas

Armored mud balls were described by Pettijohn (1949, p. 146) as large, subspherical balls of clay that are coated or armored with fine gravel. Bell (1940) showed that gravel-armored mud balls originated as clay chunks which had been eroded from rapidly undercut stream banks and which had acquired a gravel armor upon rolling down stream. Richter (1926) illustrated mud balls armored with shells.

Shell-armored mud balls (Fig. 1) are fairly common on the beaches along the Laguna

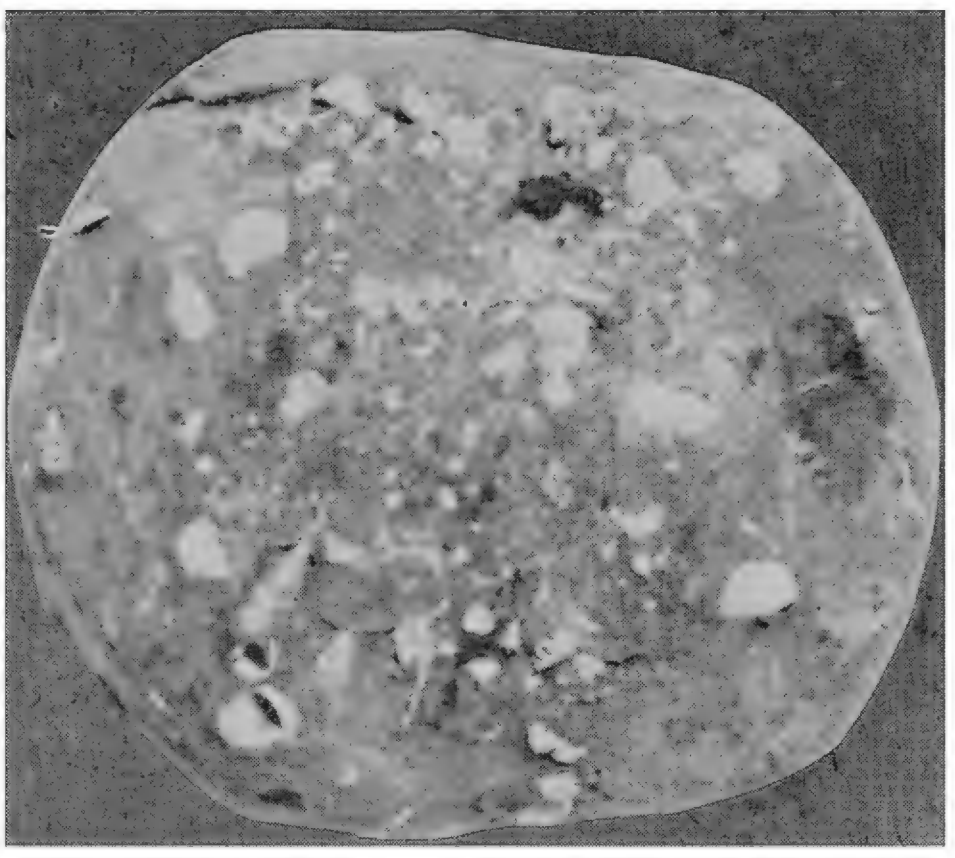

FIG. 1. A typical shell-armored mud ball from beach on Aransas Bay, Texas. Mud ball is 8 cm. long. Origin is questionable. Shells on surface have been identified by W. Rice as follows: *Cerithium variable*, *Modulus modulus*, *Bittium varium*, *Melanella sp.*, *Nassarius vibex*, *Polinices duplicatus*, *Cerithidea pliculosa*, *Odostomia sp.* (broken), *Cardita floridana*, 2 unidentified gastropods. A fish vertebra is also exposed. Photographed specimen collected by C. M. Hoskin.

Madre, Texas. They are usually oval shaped with a long axis averaging about 8 cm. (−3 Phi). These balls were observed to roll to and fro on the beach with the long axis remaining parallel to the water's edge. While migrating up and down the beach with the swash and tides, the mud balls pick up shells which adhere to their surface.

During the construction and subsequent deepening of the Intracoastal waterway, which extends the length of the Laguna Madre, sand and clay dredged from the channel were deposited on either side. The dredged material forms small islands, called spoil

banks, and flat lying strata on the shores of the Laguna Madre. Dredged material along many parts of the Laguna Madre is covered by sand dunes and vegetation which mask the artificial origin of the deposit. Waves created by wind and large ships which use the intracoastal waterway break against the dredge-deposited sediment to form beach cliffs. Exposed in many of these cliffs are mud balls similar to those found on Laguna Madre beaches. The unexposed surface of the mud balls in these cliffs are not as round as the surface projecting from the cliff indicating that the continuous lapping of waves against the cliff tends to further round the projecting side of the mud ball. It is postulated that the waves eventually undercut the cliff and free the mud balls, which are then further rounded by rolling to and fro on the beach. Accumulations of mud balls at the base of several cliffs lend support to this hypothesis. Rounding and elongation on the beach probably is due partly to abrasion and partly to water erosion.

The authors visited a dredge in operation in order to determine if the mud balls found in the dredged material were derived from sediment containing mud balls or were formed during the dredging operation. The dredge operated by laterally boring into the sediment with a steel screw several feet in diameter. The removed material was sluiced through a pipe about 16 inches in diameter and several hundred feet long. Extra lengths of pipe were added as either the place of dredging changed or the dumping area became filled.

At the time of the visit, the dredge was removing an embankment whose top was just a few inches above water level. The sediment being removed seemed homogenous with no evidence of the presence of mud balls. The sediment ejected from the pipe end, however, contained abundant mud balls (Fig. 2). During the boring operation the sediment

FIG. 2. Mud ball accumulation at end of dredge pipe-line. Mud balls average about 10 cm. in length. Top background is stream of water from pipe whose end is not discernable in upper left corner of picture.

was broken into chunks which became more or less rounded by abrasion and water action as they tumbled through the pipe. A few of the mud balls leaving the pipe had shells adhering to their outer surface, but most were barren of shells. The shells could have been picked up by the mud balls as they travelled through the pipe, but they also may have been encased in the sediment and merely exposed during the mud ball fomation.

A dredge of the type observed is probably capable of forming mud balls from any sediment it is able to cut into, providing the sediment contains sufficient clay, which seems to act as a binder. An artificial mud ball was analyzed and found to contain about 80 per cent clay. The clay was greenish, and according to Dr. Edward C. Jonas (written communication, 1958), who examined it by means of X-ray, it had a micaceous crystalline structure.

Evidently many mud balls found on beaches of the Laguna Madre and Texas bays are formed artificially by dredges. These mud balls are eroded from undercut spoil bank cliffs. Some collect a shell armor when rolling to and fro on a beach. Rolling tends to elongate the mud balls. The long axis usually parallels the water edge and is perpendicular to current or wave action.

W. Armstrong Price and T. D. Cook have observed mud balls formed by erosion of naturally deposited clay cropping out along the Laguna Madre (personal communication, 1958). The balls were most abundant immediately after a storm, and, according to Cook, naturally formed mud balls in large numbers probably are formed only during periods of rapid erosion, although, any clay shoreline can provide mud balls .

Dredged waterways and canals form a network along the coastal areas of the United States. Mud balls found in coastal areas, therefore, may have formed in the dredging process. The writers were not able to identify with assurance isolated mud balls found on beaches as having been formed by natural or artificial processes. A large number of mud balls found in place in unlithified layered sediments near dredged channels may be a clue that the deposit is probably spoil material. McKee (1958, p. 1735) interpreted rounded clay balls and cross bedding observed in strata on an island situated in the lagoon adjacent to the Port Aransas causeway, near a major channel, as indicative of strong current action in this part of the lagoon. The proximity of the channel suggests that the clay balls and cross bedding may not have been formed naturally, but are the result of dredging.

Mapping of spoil areas where artificial mud balls occur as well as those areas where clay cliffs of Recent or Pleistocene age are exposed and natural mud balls may be expected, would be helpful for determining the origin of mud balls found in these areas.

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Notes on Blanquilla Reef, the Most Northerly Coral Formation in the Western Gulf of Mexico

DONALD R. MOORE

Gulf Coast Research Laboratory, Ocean Springs, Mississippi

Introduction

Published accounts of coral reefs in the western Gulf of Mexico are rare, and little is known about this region except for a paper by Heilprin (1891) on the reef at Vera Cruz. Joubin (1912) published a map of the coral reefs of the Gulf based on Heilprin's work and on various unpublished sources. Smith (1954) published a map showing the coral reefs in the Gulf and also listed the corals found at Vera Cruz by Heilprin. The present account is the first addition in nearly half a century to the knowledge of coral reefs in the western Gulf.

Blanquilla Reef is a rather small coral reef located near the tip of Cabo Rojo in the western Gulf of Mexico. It lies offshore from Laguna de Tamiahua and about sixty miles from Tampico. Territorially it is part of the State of Vera Cruz. It is of more than ordinary interest because it is apparently the northernmost surface reef in the western Gulf. There are rocky substrates further north which do not have reefs. Thus Cabo Rojo forms the dividing line between two faunal provinces; tropical to the south, and subtropical or warm temperature to the north. Although currents are poorly known in this part of the Gulf, it is apparent that a branch of warm, clear oceanic water permits the growth of reef corals in this area.

The author and H. H. Hildebrand visited Blanquilla Reef April 26 and 27, 1955. The trip from the mainland was made in a small skiff with an outboard motor, which held little besides its passengers. The author contented himself with a small collection of invertebrates, and with some observations on the structure of the reef. These observations were made while wading in shallow water, and swimming and diving in deeper water.

Observations

Blanquilla Reef lies approximately three miles southeast of Cabo Rojo (21°33′N.–97°17′W.). The depth is about fourteen fathoms between the reef and the mainland, and fairly deep water is found very close to the lee side of the reef. A rough estimate of the size of the reef would be about eight hundred yards long in a north-south direction, and five or six hundred yards wide. On the highest point, the Mexican government has erected a concrete monument with an automatic light as an aid to navigation. The surrounding area is awash at low tide and is paved with loose coral cobbles. There is an extensive shallow water area around the high portion which gradually deepens in all directions toward the reef edge. This edge is poorly defined on the windward (east) side, but there is a small cliff with about a ten foot drop on the west side.

Live coral was rare on the seaward side, but became more common along the west side and was flourishing along the edge of the cliff. Small "heads" of *Siderastrea siderea* and *Diploria clivosa* were living in shallow water not far from the monument. *Acropora palmata* was fairly common in slightly deeper water close to the western edge. *A. cervicornis* was also found in this area, but in much smaller quantity than *A. palmata. Montastrea annularis* formed large massive colonies along the cliff edge, and was quite common. *M. cavernosa* was uncommon, and all colonies examined were found in deep water beyond the cliff. A few small *Porites furcata* were living in the *Acropora* zone. A very flourishing growth of coral heads in deep water below the cliff was made up mainly of two species of *Diploria* (*strigosa* and *labyrinthiforms?*).

This reef differs considerably in structure from the reefs off the Florida Keys. It faces a long reach of open water, over a thousand miles in the northeastern sector. Storm waves from this direction build up to near maximum power and velocity. As a result, the seaward side is almost a flat expanse of bare coral rock with a very gradual slope toward the open sea. It is covered by a pink encrusting alga, and the burrows of a sea urchin. The Florida reefs do not have such a wide reach of open water and are protected somewhat except in hurricane seas, by the proximity of the Bahama Islands and their associated shallow banks. The seaward side of such reefs has considerable relief and quite a bit of live coral, and tends to slope down at a fairly steep angle. The landward side of Blanquilla Reef is also quite different from Florida reefs. The bottom descends to about ten fathoms within about a hundred yards of the western edge, while the Florida reefs usually have sand bottom from ten to thirty feet deep on the landward side. Differences in reef structure are apparently attributable to different physical conditions between the two areas.

Most of the invertebrates were small and easily overlooked, compared to the massive colonial corals. However, a conspicuous constituent of the fauna, the sea urchin *Echinometra lucunter*, was very numerous on the seaward sloping portion of the reef. All were living in burrows which they had excavated by scraping algae from the rock. This burrowing habit enables the urchin to live on the exposed seaward side despite the action of the larger waves. Dr. Voss of the Miami Marine Laboratory indicates that *Echinometra lucunter* forms a distinct zone in semi-protected shores of the Florida Keys and the Bahamas. Another large sea urchin, *Diadema antillarum*, was found under rocks or along the edge of the cliff on the west side, but it was not common. Other echinoids were *Eucidaris tribuloides* found under rocks, *Tripneustes esculentus* scattered in deep water on the west side, and a starfish, *Linckia guildingi*, on rocks. Brittle stars were observed, but none were identified with certainty. A small armoured holothurian probably *Thyonepsolus braziliensis*, a shallow water West Indian species, was found when a piece of coral rock was closely examined in the spring of 1958. Some traces of color remained. It was apparently bright red when alive, and was evidently overlooked due to its similarity in appearance to *Homotrema rubra.*

Alcyonarians were scattered and rather scarce. Only three species were observed living on the reef. They were *Antillogorgia acerosa, Plexaura flexuosa,* and *Plexaurella dichotoma.*

The remaining animals identified were all mollusks except for one unusual protozoan, *Homotrema rubra.* This is a bright red encrusting foraminiferan found attached to the

underside of rubble on reefs. It is large for a protozoan and conspicuous, for its color contrasts with the light colored rock. Although common on reefs in the West Indian region, it is not confined to shallow water, and may be found living to depths of forty fathoms or more off the Alabama coast (personal observation).

The Mollusca identified were also common West Indian species found on coral reefs. The gastropods *Thais deltoidea* and *Astraea* sp. were living out in the open on coral rocks, but other species such as *Drupa nodulosa*, *Cerithium literatum*, and *Pisania pusio* were only found under rocks. Pelecypods included the widespread species *Arcopsis adamsi*, *Isognomon radiata*, *Lima scabra*, and *Lithophaga aristata*.

Some gastropods common on Florida reefs that were not found on Blanquilla include *Astraea caelata*, *Conus regius*, *Cypraea cinerea* and *Mitra barbadensis*. *Corallipphila abbreviata* is usually found living on the coral, *Acropora palmata*, but none could be found on this reef. *Strombus gigas*, one of the largest of the West Indian gastropods, was also absent, but a small specimen of the giant horse conch, *Pleuroploca gigantea*, was collected.

The fauna of Blanquilla Reef appears scanty when compared with that of the Florida reefs. However, this reef is a small one and is lacking a number of ecological zones in which corals and other invertebrates are found living in the Florida Keys. A number of corals in the Florida area occur usually in shallow water behind the main line of reefs. Lobos Island, a few miles south of Blanquilla Reef, may have a larger and more varied fauna, and should prove a fruitful field for investigation. Another factor to be considered is that this list of fauna is based on a cursory examination and hurried collection.

The close relationship of the Blanquilla Reef fauna with the rest of the West Indies is without question. Almost all of the species listed are also found on the Florida reefs and much of the West Indian region. Nearly all of the species under consideration have pelagic larvae and establish themselves wherever natural conditions are favorable. Although conditions are apparently not suitable for the best development of a coral reef off Cabo Rojo, the minimum requirements are met for at least some tropical species.

List of Species Identified

Many of the larger animals were identified in the field but most of the smaller organisms were collected and identified later. In the case of corals of which identity was doubtful, an attempt was made to collect a small colony for more accurate identification in the laboratory. In the following list an asterisk indicates field determinations only. The author alone is responsible for the names in the list, except the Alcyonarians, which were identified by F. M. Bayer. The specimens collected, except the Alcyonarians and a holothurian, were deposited with the invertebrate collection at the Institute of Marine Science, Port Aransas, Texas. The Alcyonarians were sent to the United States National Museum.

PROTOZOA

Foraminifera

Homotrema rubra Lamarck

COELENTERATA

Corals

Acropora palmata Lamarck
Acropora cervicornis Lamarck
Siderastrea siderea Ellis & Solander
Diploria clivosa Ellis & Solander
Diploria strigosa Dana
Diploria labyrinthiformis Linne? *
Montastrea annularis Ellis & Solander
Montastrea cavernosa Linne *
Astrangia brasiliensis Vaughn?
Mycetophyllia lamarckana Edwards & Haime?
Porites furcata Lamarck *

Alcyonarians (Identified by F. M. Bayer)

Antillogorgia acerosa Pallas
Plexaura flexuosa Lamouroux
Plexaurella dichotoma Esper

MOLLUSCA

Gastropods

Mitra nodulosa Gmelin
Nitidella ocellata Gmelin
Charonia variegata Lamarck
Columbella mercatoria Linne
Ocenebra aberrans C. B. Adams
Thais deltoidea Lamarck
Engina turbinella Kiener
Acmaea jamaicensis Gmelin
Cerithium literatum Born
Astraea sp.
Conus mus Hwass
Tegula semigranosa A. Adams
Drupa nodulosa C. B. Adams
Pisania pusio Linne
Leucozonia nassa Gmelin
Bulla occidentalis A. Adams
Aplysia dactylomela Rang *

Pelecypods

Arcopagia fausta Pultney
Isognomon radiata Anton
Arcopsis adamsi E. A. Smith
Arca umbonata Lamarck
Barbatia candida Helbling
Lima scabra Born
Lithophaga aristata Dillwyn

ECHINODERMATA

Echinoids

Diadema antillarum Philippi *
Echinometra lucunter Linne *
Eucidaris tribuloides Lamarck *

Asteroids

Linckia guildingi Gray *

Holothurians

Thyonepsolus braziliensis Theel?

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Evidence for Fossil Bacteria in Phosphate Rocks

CARL H. OPPENHEIMER

Institute of Marine Science, Port Aransas, Texas

One of the most difficult tasks in micropaleontology is to differentiate fossil bacteria from artifacts. However, several reports have appeared which seem to offer conclusive evidence for the existence of such fossil bacteria. A recent annotated bibliography by ZoBell (1957), lists 62 references on fossil microorganisms. One of the earliest reports describing fossil bacteria (Renault, 1895) suggested that the organisms may have been significant in the formation of specific types of sediment. Renault attempted to relate the morphological forms he found with known species of bacteria of the era, e.g. *Bacillus tieghemii*. Barton and Jones (1948) have published electron micrographs of Oligocene rocks showing possible remains of bacteria. Thread molds and bacteria in the lacunar spaces of fossilized vertebral bone have been found in the Devonian by Moodie (1920).

Usually the fossil remains of bacteria have been found in cracks and pore spaces of rocks which have been filled with organic matter. In these instances it is difficult to determine whether the bacteria were indigenous forms or active in the geological processes.

The materials examined for this report were collected by M. N. Bramlette, of the Scripps Institution of Oceanography, from a phosphate mine at Gafsa, Tunisia, and from Ocean Island in the Gilbert group in the South Pacific Ocean. Bramlette (1955) states

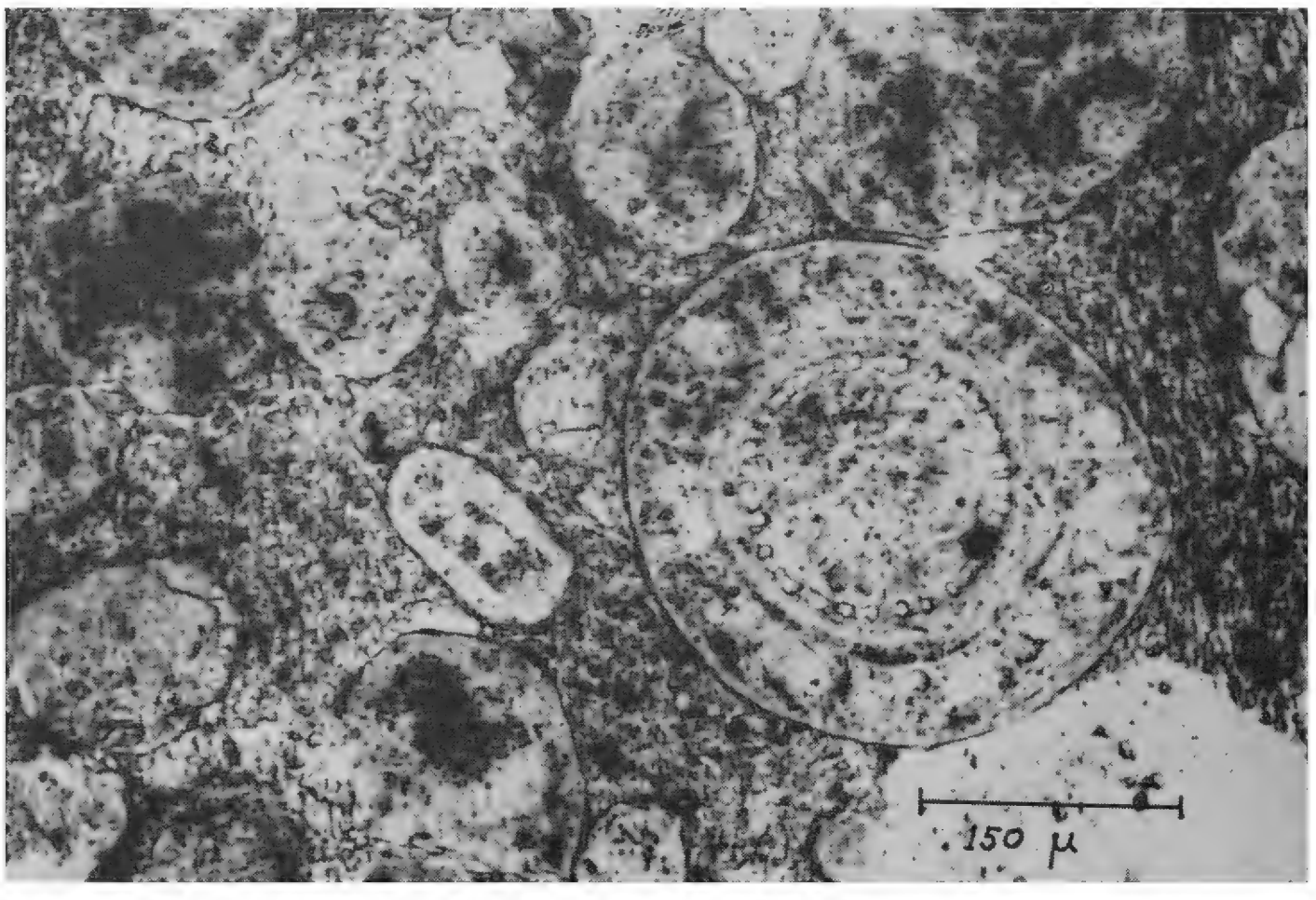

FIG. 1. Photomicrograph of a Thin Section of Phosphate Rock from Tunisia Showing Fecal Pellets with a Radiolarian? Inclusion (X250).

that "the phosphate rock from Tunisia is typical of much of these North African deposits which form widespread beds in the early Tertiary of the region. The formation of the phosphate rock must have been during the time of deposition of the associated strata, some 60–70 million years ago." The phosphate rocks consist of small round bodies with little interstitial cementing material. Thin sections were made by the usual grinding procedure. The sections were examined by bright field and phase microscopy. The round and oval bodies (Fig. 1), having an average diameter of 150 microns, are assumed to be ooids (individual oolites) and phosphatized fecal pellets from some small organism. Many of the pellets contain broken fragments of diatoms, radiolarians and foraminifera. Some contain unbroken organisms such as the radiolarian seen in figure 1. Moore (1939) describes some of the fecal pellets found in marine deposits.

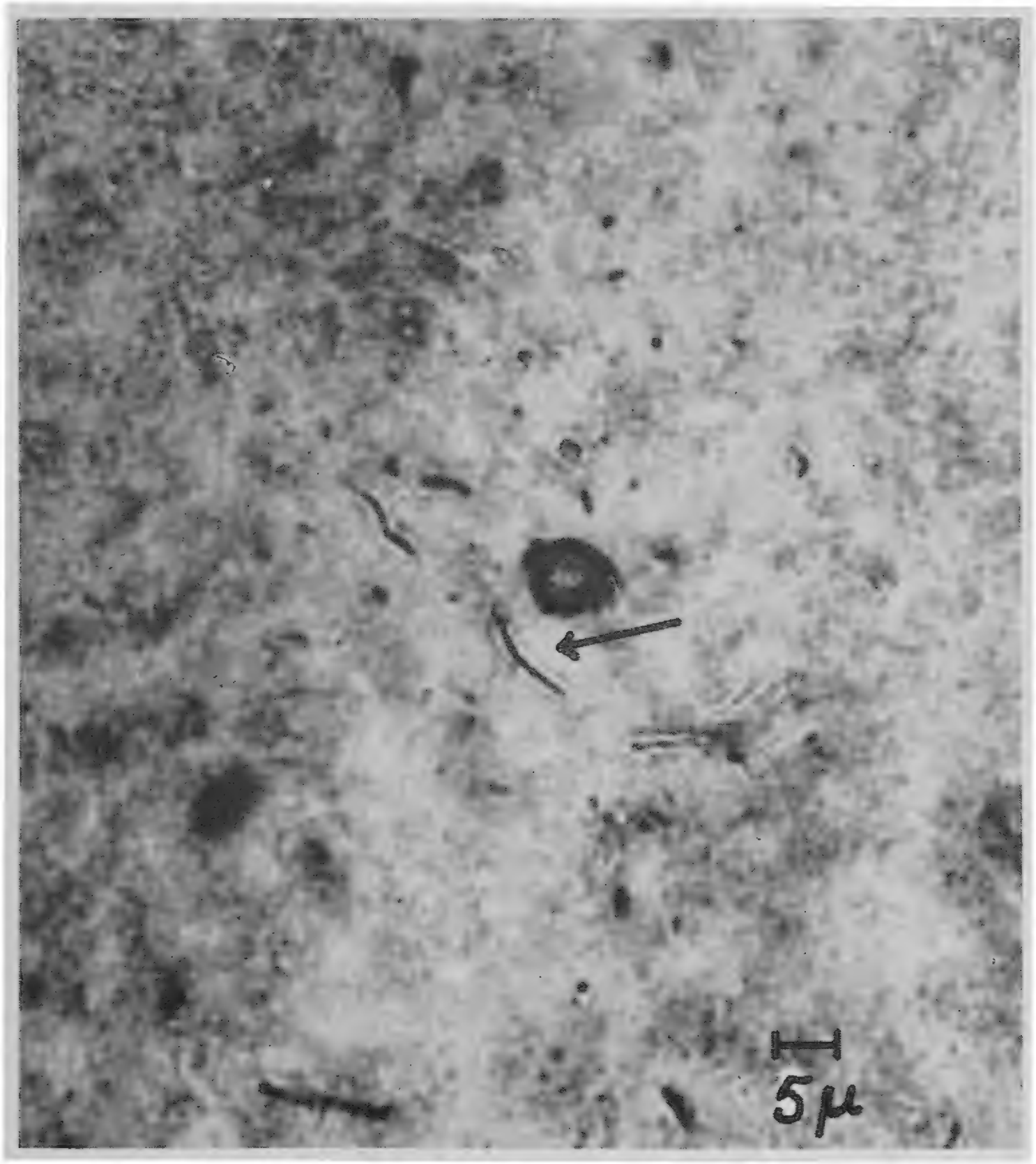

FIG. 2. Photomicrographs by Phase Microscope of Fecal Pellets in Thin Sections of Phosphate Rock from (a) Tunisia and (b) Ocean Island. The elongate dark bodies (arrow) are assumed to be Fossil Bacteria. Figure 2a above.

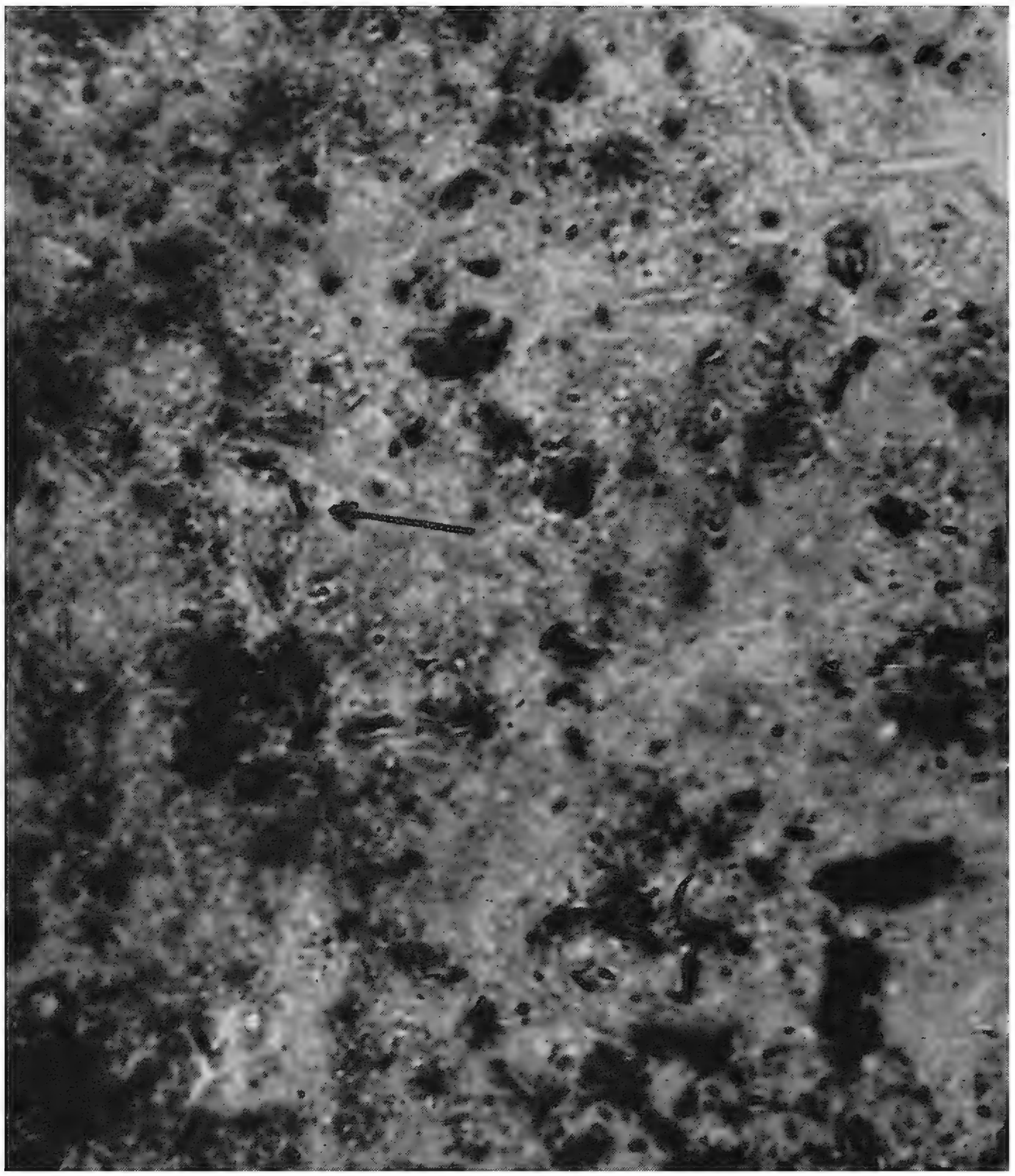

FIGURE 2b.

Modern fecal pellets contain many bacteria and therefore, fossil fecal pellets are not an unlikely source of fossil bacteria. Pettijohn (1949) states that small granules and oolites are always present in phosphorite sediments. In some phosphorites, where phosphorus has been precipitated, a fossil fragment serves as a nucleus thus producing a radial structure. Pettijohn describes the formation of ooids by the preciptation of phosphorus which sometimes initially cements small particles of organic matter and fragments of organisms. If this is true, then bacteria must certainly be present and associated with the organic matter and particles. It is difficult to distinguish between fecal pellets and ooids and, therefore, the forms described in this paper will be referred to as pellets even though the author has assumed them to be fecal pellets.

Microsopic examination of thin sections of Tunisian rock were made. At magnifications of 1000 many small uniform rod shaped objects of a diameter of 0.5 to 1 microns were

seen which resemble bacteria. The length of the forms varied from 1 to 3 microns, the ends were rounded and chains of two were present. Figure 2a illustrates the size and shape of the small forms. It is difficult to obtain good photomicrographs of the thin sections because of depth of field limitations. Therefore, the elongate objects seen in the photomicrographs in figure 2 represent only a few of the many found in the sections of rock. It is presumed that the forms represent bacteria which were incorporated in and, or, were decomposing the organic material of the pellets at the time of sediment deposition. Bacteria must have been present during or before phosphatization. Cultural techniques were not used to determine whether the bacteria were still alive because it would be difficult to determine if bacterial growth was due to bacterial contamination in the interstitial spaces or the fossilized forms.

The abundant bacteria-like forms were found primarily inside the pellets associated with other inclusions. It is unlikely that the forms are due to contamination during the sample preparation because of their abundance and the fact that pellets or oolites have a rather hard impermeable outer shell which would discourage bacterial entry. However, it is possible that bacteria could enter the rock formation when the rocks were more permeable than at present. Some bacteria were seen in the spaces between the pellets and could possibly be contaminants of a later geological date or from the laboratory treatment.

Bramlette (personal communication, 1955) reports that, "the sample of phosphate rock from Ocean Island came from one of the open pit mines of the higher central part of the island. The blanket of ore is due to phosphatization of an original calcareous reef formation." Thin sections of this rock examined at 1000 diameters had many of the bacteria-like forms which are shown in figure 2b. Ift it is assumed that these are fossilized bacteria, they were presumably present during the time of the reef formation and probably not earlier than the later Tertiary or Pleistocene.

This is a note of academic interest to be added to the growing evidence for fossilized bacteria, the existence of which is difficult to prove. However, the recent work by Abelson (1956), which demonstrates the presence of amino acids in ancient shells, certainly suggests that some constituents of protoplasm might persist during geological time and it seems reasonable to assume that bacteria would be represented. As new techniques of organic analysis are developed it might be possible to identify the protoplasm of small organisms such as bacteria in ancient sediments and rocks.

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A Bacterium Causing Tail Rot in the Norwegian Codfish

CARL H. OPPENHEIMER[1]

Institute of Marine Science, Port Aransas, Texas

During the spring of 1953, while at the University of Oslo Biological Station a study was undertaken to determine the causative agent of the so-called "Tail Rot" disease of the Norwegian codfish *Gadus callarias*. A similar disease in the sea herring, *Clupea harengus*, is caused by a gram negative pleomorphic rod which has not been characterized (Sindermann and Rosenfield, 1954). A partial review of other marine fish diseases of bacterial origin is given by Oppenheimer and Kesteven (1953).

In Oslofjord near Oslo live cod are kept in submerged wooden cages in the fish markets and tail rot is quite prevalent in these fishes. The water temperature in the fjord varied between 5° and 9° C. The infection usually started on the margins of the fins or tail and produced a characteristic whitish color (Fig. 1). The infection progressed inward from the edge of the fin or tail and soon involved the integument and muscle tissues. In advanced stages of the disease only the spines of the tail or fins re-

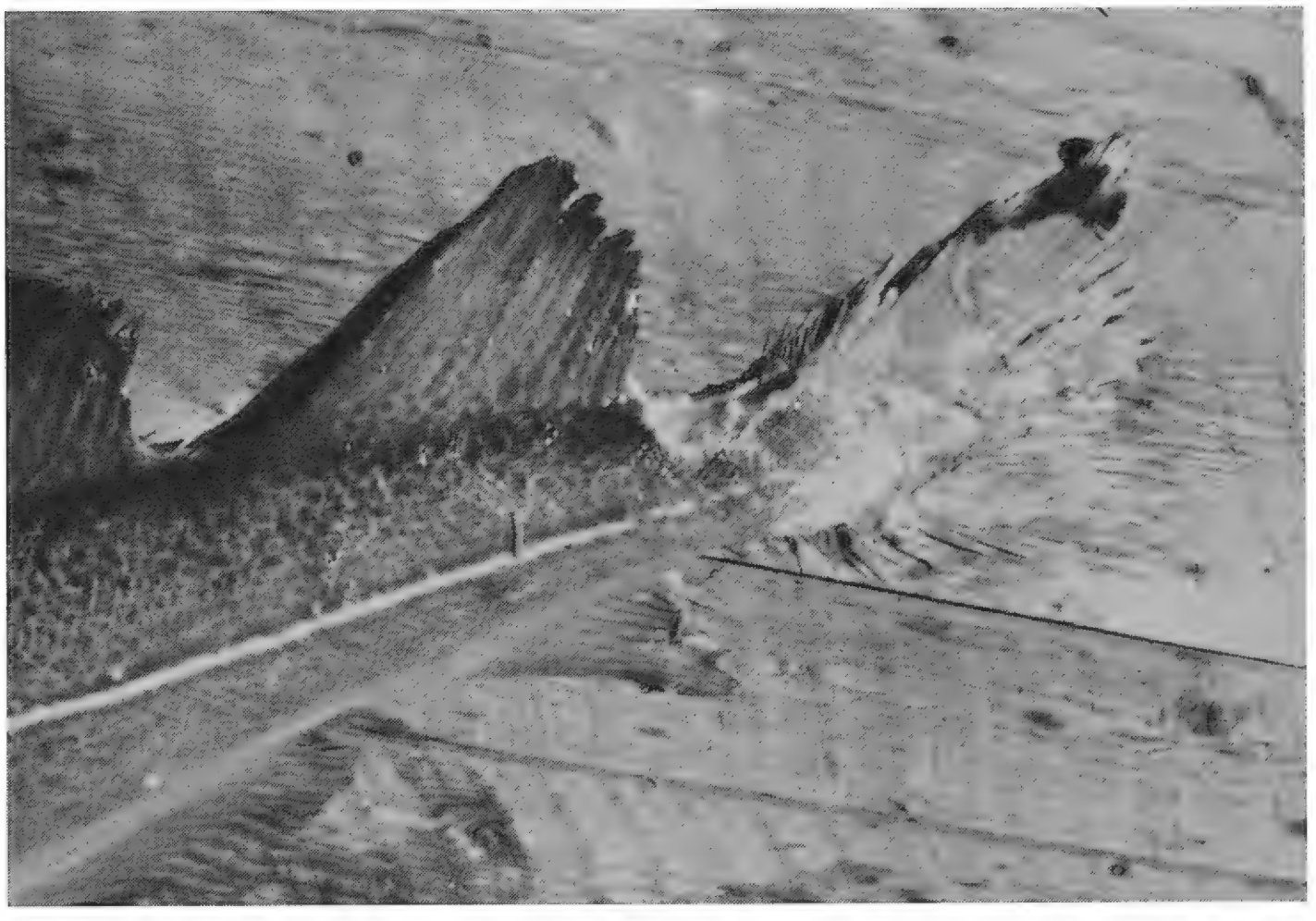

FIG. 1. Typical appearance of "Tail Rot" disease of the Norwegian codfish.

[1] Fulbright Fellow, 1952–53.

mained, bleeding was noted and other areas of the integument developed lesions. Concurrent examination of the blood of the fish in advanced stages of the disease demonstrated motile rod-shaped bacteria suggesting that the infection was systemic. The fish usually died within 48 hours after lesions appeared and the muscle became infected.

Experimental Methods

Material from the lesions of the integument and tail regions of diseased living fish was examined by phase microscopy and by cultural methods. Large numbers of motile rods and cocci were present. Material from the lesions was infective when inoculated into the fleshy base of the tail of healthy fishes. The material from the lesions was streaked on petri plates containing sea water nutrient agar (Medium 2216, ZoBell, 1946) enriched with codfish extract. The plates were incubated at 15° to 18° C.; i.e. approximately 10° C. warmer than the aquarium water. The bacterial colonies which appeared on the plates after incubation were purified and tested for pathogenicity by the inoculation of a dilute suspension of the bacteria into healthy fishes. One microorganism was isolated in pure culture which produced the characteristic tail rot when inoculated into the skin at the base of the tail of healthy fish. A small lesion soon appeared at the site of inoculation and the infection spread to the tip of the tail and then progressed as the disease did in nature. The tail rot was marked after 24 hours when lesions typical of the advanced disease appeared and death occurred in approximately three days. A microorganism identical with the original inoculated culture was reisolated from the lesion of the experimental fish. The reisolated culture produced the typical disease.

The characteristics of the pathogenic bacterium were determined by "Standard Methods Procedures" except that 75 percent sea water was substituted for distilled water. Litmus milk was made with distilled water since sea water reacted with the medium. Incubation was at 16° C.

Description

Short rods: 1 x 2 microns occurring singly, in pairs and in short chains. Motile with single polar flagellum. Gram Negative.

Agar plate: Round with entire edge, moist, glistening, creamy white color, slightly opaque.

Gelatin stab: Crateriform liquefaction at 7 days.

Broth: Turbid, no pellicle.

Potato: No growth.

Litmus milk: No growth.

Starch: Not hydrolyzed.

Ammonia produced from nitrates.

Indole not formed.

Distilled water nutrient broth: No growth.

Acid from maltose and saccharose. No acid or gas from glucose, lactose, mannitol, salicin or glycerol.

Sensitivity tests with antibiotics indicated that growth of the organism was inhibited in vivo and in vitro by penicillin, streptomycin, chloromycetin, neomycin and polymyxin.

Conclusions

The above description places the bacterium in the genus *Pseudomonas* according to Bergey's Manual of Determinative Bacteriology, 6th Ed. The description applies to no other described organism. The culture was lost during transit back to the USA and therefore other cultural characteristics were not determined. The above description is not adequate to name a new species, but may be useful to other microbiologists working with "tail rot" diseases of fishes.

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An Incidence of Pink Oysters in Galveston Bay, Texas

Richard Y. Morita[1]

Department of Biology, University of Houston, Houston, Texas

During the middle of December, 1955 an incidence of pink oysters was brought to the attention of the investigator by Mr. G. J. Brittain. Engineer Assistant, Division of Sanitary Engineering, State Department of Health, Harris County Health Unit).

A pink discoloration was noted in the juice of shucked oysters taken from Redfish Reef, Galveston Bay. These shucked oysters were obtained from many of the oyster houses around Seabrook, and had been placed in pint, quart, and gallon containers. According to the oyster house operators, this condition was confined to the oysters taken from Redfish Reef.

Normally oyster juice has a colorless translucent appearance. However, pink discoloration of the oyster renders them unsightly and unfit for food (Tanner, 1944). The occurrence of pink oysters has been attributed to the presence of yeasts (Tanner, 1944) and to the presence of carotenoids, from the food of the oysters, which have been concentrated in the tissue and which bleed from the tissue when the oyster is shucked (Adam, 1949). Since microorganisms may cause the pink discoloration, a bacteriological examination was performed on the oyster juice.

Slides were made from the oyster juice to determine whether or not one morphological type of organism was predominant. Slides that were Gram stained revealed a large number of Gram negative, short, straight rods, but no yeast cells were demostrated. Yeast cells were not demonstrated on slides stained with methylene blue.

Routine plate counts were made from fresh pooled oyster juice, obtained from oysters from Redfish Reef, which had been standing in the oyster houses for about four days. This freshly prepared oyster juice was collected as aseptically as possible. It was used in preference to oyster juice from previously shucked oysters that were already in containers to obviate gross contamination by the shuckers. Oyster juice collected with this method had a slight pink discoloration. Employing a sea water medium, 2216E (ZoBell, 1946), peptone (Difco), 5 g.; yeast extract (Difco), 1 g.; ferric phosphate, 0.1 g.; aged sea water, 1000 ml.; pH 7.5, a plate count of 180×10^8 bacteria per ml. was obtained, of which 130×10^8 bacteria produced a dark pink pigment. A plate count of 30×10^7 bacterial per ml. was obtained from the oyster juice, using nutrient agar peptone (Difco), 5 g.; beef extract (Difco), 3 g.; distilled water, 1000 ml.; pH 7.0, of which 21×10^7 bacteria per ml. produced a dark pink color. Incubation of the plates was performed at room temperature.

Pure cultures were isolated from the oyster juice. Microorganisms that produced a dark pink or reddish color were subjected to routine bacteriological tests to determine,

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[1] Present address: Department of Bacteriology, University of Nebraska, Lincoln, Nebraska.

if possible, the genus and species. All of the isolated microorganisms gave the following results:

Gram stain: Gram negative, short, straight rods (24 hour culture).
Spore stain (Wirtz): No spores (48 and 72 hour cultures).
Agar colonies: Granular, circular, thin, white becoming dark pink in 3 or 4 days.
Broth: Turbid, turning dark pink in 3 or 4 days.
Indole not produced.
Nitrites from nitrates.
Odor of trimethylamine.
Aerobic and facultative anaerobic growth.
Litmus milk: Acid, soft curd, dark pink growth.
Pigment: Not readily soluble in water, soluble in alcohol and ether.
Glucose broth: No gas.
Acetylmethylcarbinol is produced.
Gelatin: No pellicle.

From the above data the organisms would be classified as *Serratia marcescens.*

According to Bergey's Manual of Determinative Bacteriology (Breed, *et al.*, 1957) *Serratia marcescens* is found in water, soil, milk, foods, silk worms, and other insects. Other species of *Serratia* have been implicated in the reddening of codfish (Tanner, 1944). Since *Serratia marcescens* is normally found in soil and water, the utensils and water used in the oyster houses were checked for *Serratia marcescens.* Results were negative and, therefore, ruled out the possibility of gross contamination of oysters from the oyster houses.

Oysters from other sections of Galveston Bay were obtained from the oyster houses. Freshly pooled oyster juice was prepared and checked for the presence of *Serratia* (as evidence by a pink or red colony) by the plate count method. Medium 2216E was used for checking the presence of *Serratia* colonies. A plate count of 35×10^6 bacteria per ml. was obtained from the oyster juice. Plates made from a 1:1,000,000 dilution of this oyster juice had no red or pink colonies.

The oyster shuckers apparently did not notice a discoloration when shucking oysters. The discoloration was more evident after the shucked oysters had been allowed to stand. Evidently the time interval served as an incubation period for the growth of *Serratia.* Difficulty of securing proper samples, as well as arriving on the scene late, prevented the investigator from making a more complete bacteriological investigation.

It is suggested from the data that the occurrence of pink oysters resulted from an infection of *Serratia marcescens.*

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The Drop-Net Quadrat, a New Population Sampling Device[1]

Thomas R. Hellier, Jr.

Institute of Marine Science
The University of Texas
Port Aransas, Texas

Determining the biomass of fish in a prescribed area is one of the most difficult problems in studies of fish productivity. Many methods have been proposed for this purpose, such as tagging and clipping, determinations of catch per unit effort, electrical sampling, and in small areas draining or poisoning. Although these methods have often been used and modified for specific areas and studies, size selection is usually a problem (Carlander, 1956). A survey of the fisheries literature indicates that no method is applicable to all situations. The above methods, their advantages and their limitations, are described by Haskell (1940), Smith (1940), Krumholz (1943), Ricker (1943, 1948a, 1948b, 1956), Shetter and Leonard (1943), Rounsefell and Kask (1946), Carlander (1948, 1956, 1958), Delury (1951, 1958), Meyer-Waarden (1957), and many others. None of these methods seemed completely suitable for studies in broad, shallow marine bays.

This paper describes a new method being used for a fisheries population study in the large Laguna Madre of Texas. General biological features of this shallow hypersaline bay were recently described by Simmons (1957). It is hoped that this new method, the drop-net quadrat, will eliminate much of the selectivity inherent in more standard methods .

The author acknowledges the services and generous contribution of ideas from members of the staffs of the Institute of Marine Science and the Marine division of the Texas Game and Fish Commission in Rockport.

A somewhat similar trap was used in a farm pond in a class project at A and M College by Mr. William B. Wilson in 1950. The trap covered 225 square feet and operated with sliding panels (personal communication).

Description of Method

The drop-net quadrat method of population sampling consists of surrounding a large quadrat (100 ft. by 100 ft.) with a small mesh net (Fig. 1). This net is supported by a steel cable suspended approximately 3 feet above the surface of the water from eight piling. The piling may be easily placed or removed by a ¾ inch jet of water supplied at 20 to 30 pounds pressure per square inch. A heavy chain

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[1] These studies were aided by the Texas Game and Fish Commission as part of the project: Productivity of the Striped Mullet in the Laguna Madre of Texas, a study of herbivores in a bay system, Howard T. Odum and Thomas R. Hellier, Jr.

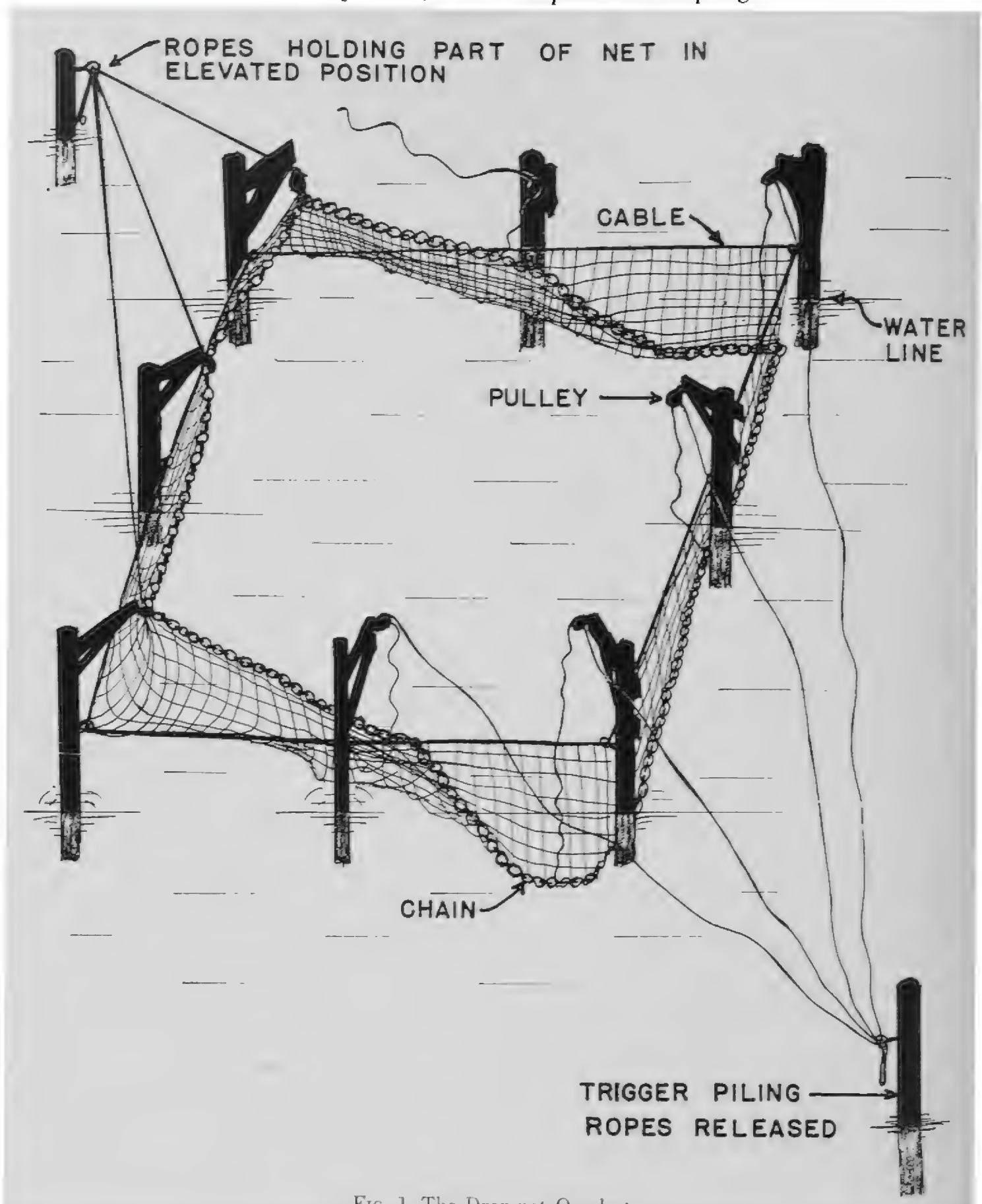

FIG. 1. The Drop-net Quadrat.

(1 pound per foot) is used for a lead line on the net. A line is secured to the chain at each piling. These lines are passed through pulleys located on crossarms at the top of the piling, and the net is hoisted clear of the water. After the lines are secured to a trigger mechanism the net is ready to drop. The area is left undisturbed for several hours after the net has been rigged. The trigger is then released, freeing the lines, and the net drops into place. This method effectively and rapidly isolates the quadrat. The quadrat is then seined repeatedly with a 120 ft. bag seine until all of the fish are removed.

Discussion

The drop-net quadrat is at present adapted for a relatively shallow homogeneous area of Texas bays, but might also be used for quantitative collection of other estuarine and coastal bay areas. Initial trials of the method have been conducted with netting of two mesh sizes on a ¼ acre quadrat, and on a small quadrat (1/16 of an acre) with small mesh netting (¾ inch stretch).

The results of the first trials are presented in Table 1. Even though these early trials

TABLE 1

Yield of Fishes from Drop-net Quadrat in Pounds per Acre of Preserved weight

	¼ acre quadrat,[a] 3 inch stretched mesh	1/16 acre quadrat,[b] ¾ inch stretched mesh	¼ acre quadrat,[c] ¾ inch stretched mesh
No. of Trials	6	6	6
Average yield, per trial	25.5 (2.9g/M²)	54.6 (6.1g/M²)	121.3 (16.6g/M²)
Yield of highest single trial	73 (8.2g/M²)	145.3 (16.3g/M²)	176.2 (19.8g/M²)
Yield of lowest single trial	3.2 (0.4g/M²)	5.4 (0.6g/M²)	64.5 (7.2g/M²)

[a] Principal fish species taken: *Galeichthys felis, Mugil cephalus, Cynoscion nebulosus, Micropogon undulatus, Pogonias cronis, Sciaenops ocellata.*

[b] Principal fish species taken: *Anchoa mitchilli, A. hepsetus, Menidia beryllina, Mugil cephalus, Leiostomus xanthurus, Micropogon undulatus, Lagodon rhomoides.*

[c] Principal fish species taken include all of above.

were necessarily selective, because the large mesh in one set of trials captured only the largest fish and the small area of the quadrat in the other selected against the larger fish, the data obtained indicates that a ¼ acre trap with ¾ inch stretched mesh netting is adequate to take all size groups. There are now several traps located in representative areas of the Laguna Madre which are being tripped at regular intervals. These are the basis for continuous estimation of the biomass, not only of fishes, but of some invertebrates also. The initial data from these traps (¼ acre; ¾ inch stretched mesh) also are presented in Table 1.

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Fluctuations in the Relative Abundance of Sport Fishes as Indicated by the Catch at Port Aransas, Texas

1952–1956

VICTOR G. SPRINGER[1] AND JACQUES PIRSON

Institute of Marine Science
The University of Texas

Introduction

Port Aransas is a small coastal town located at the mouth of Aransas Pass inlet on Mustang Island, which is adjacent to the Texas mainland (Fig. 1). One of its primary industries is sport fishing and many of the inhabitants derive their livelihood directly or indirectly from it. Unfortunately quantitative data on sports fishing are scarce everywhere and especially in the western Gulf. This report of records gathered at Port Aransas provides a view of the annual cycle.

The Port Aransas Tourist Bureau was established in 1951. One of its functions is to keep the public aware of the varieties and numbers of fishes being caught in the area. This function has been served by the dissemination of a weekly mimeographed bulletin summarizing the catches of sport fishermen as total numbers of fishes caught of each species. The sport fishes reported at Port Aransas are those caught at the jetties of the Lydia Ann Channel or in the open Gulf from piers and charter boats. Information regarding catches is supplied to the Bureau by local establishments integrally associated with the area's sport fishing. In recent years these sources of information have been primarily Mathews Sportsman's Headquarters, the Island Charter Service, Fisherman's Wharf, and Pappy and Mammy's; all are located within Port Aransas. Compilation of the catches and publication were originally under the supervision of Mrs. G. L. Webb but are presently supervised by Mrs. Norma Skinner. The catch, which is reported, is only a part of the total catch at Port Aransas. What percent is reported is not known.

ACKNOWLEDGMENTS

Sincere appreciation is due Mrs. Norma Skinner for her patience and alacrity in providing us with information necessary to the completion of this study. We wish also to thank the numerous residents of Port Aransas who offered us pertinent information on our subject. Dr. H. T. Odum called our attention to the possibility of the study and offered suggestions concerning the manuscript.

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[1] Present address: Florida State Board of Conservation, Marine Laboratory, Maritime Base, Bayboro Harbor, St. Petersburg, Florida.

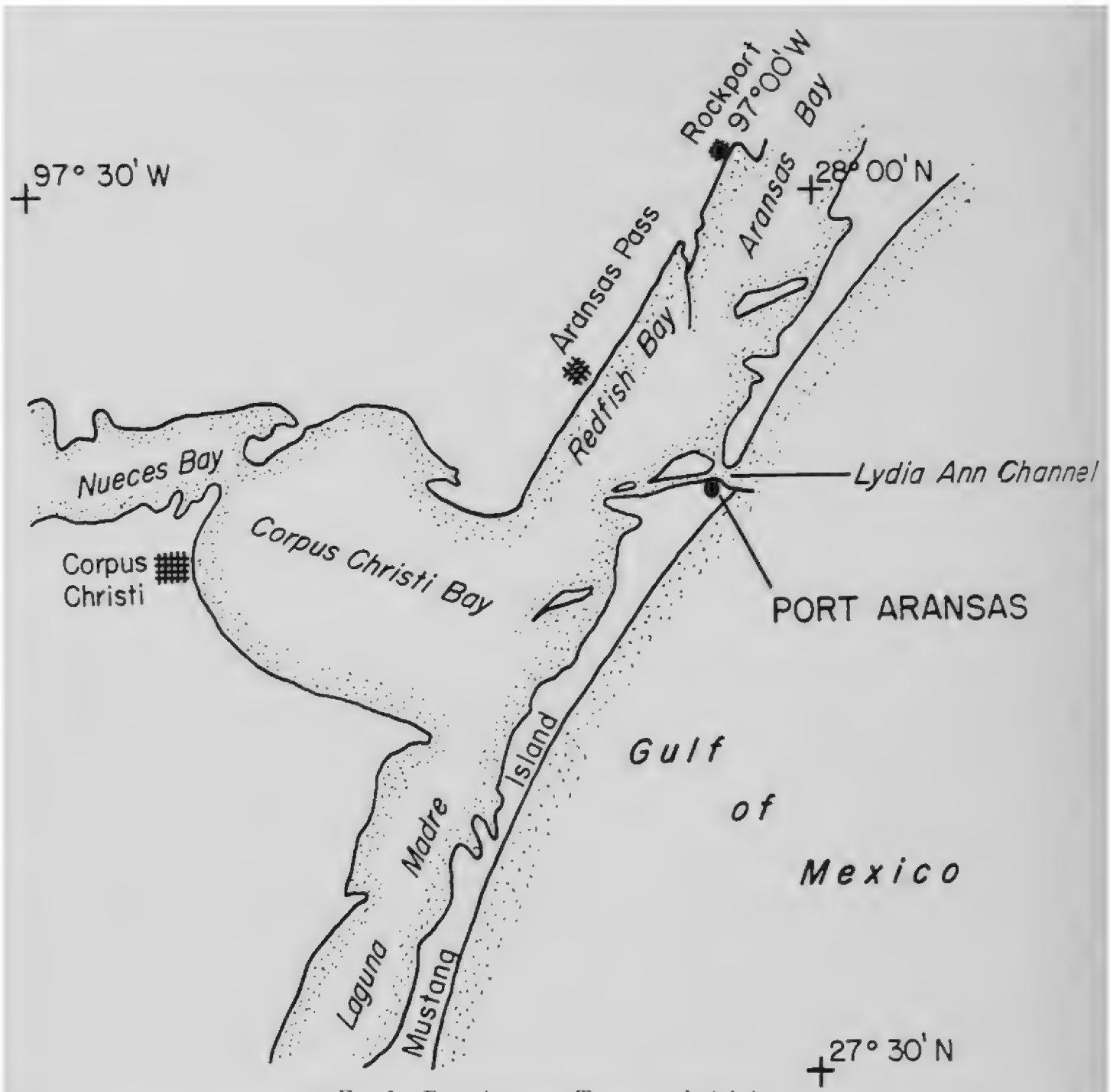

FIG. 1. Port Aransas, Texas, and vicinity.

PROBLEMS IN ESTIMATING THE RELIABILITY OF THE DATA

Evaluation of the completeness with which catch reports are made shows there has been considerable variation in the methods used. Some of the participating organizations estimate that their reports are as much as 95 percent complete, while others admittedly state their reports contain only the best two or three catches each week out of some hundreds. Some omit certain fishes from their reports (*i.e.* catfishes).

Report sheets are missing for sixty-five of the two hundred and sixty-one (or about 25 percent) weekly periods covered by this study. However, all but one of the months during the period are represented by at least one report. The most serious deficiencies occur for the following dates: June 25–July 15, 1952; August 27–September 16, 1952; December 10, 1952–January 1, 1953; April 29–May 28, 1953; September 15–October 5, 1954; December 8, 1954–January 5, 1955; March 31–April 27, 1955; and May 5–May 30, 1955.

No reports are issued the last two or three weeks of December in compliance with Post Office Department requests that bulk mail be withheld during the holiday mail rush.

No uniform method of dating the reports has been maintained over the years. Sometimes part of the last week of the year is included with the first week of the next year;

other times recording starts with the first week of the year. Frequently report periods are three or four days only; occasionally there is a gap of two or three days between the dates covered by the reports. Dates often overlap (*i.e.* January 1 to 7 followed by January 7 to 14). In most of these instances the catches for the overlapping days would be split between the two reports, probably because the information was received too late to be included at the time of the first publication.

Graphs

As the reports for certain weeks of certain months are not strictly comparable from year to year, it was necessary to devise a means of graphing which would most accurately portray the tendencies of the fishery. For the purpose of this study the policy has been to recognize the first week of the year as the first week which contains reports only for that year, and the last week of the year as the last week which contains reports for that year whether or not the first few days of the next year are included. The same method applies to weeks that include days from two months. The reports are published approximately fifty times a year and despite the fact that the weeks are not exactly comparable, they are listed on the graphs in accordance with their numerical sequence, one year below the next. The graphs report the numbers of fish caught for each period. If the scale is too low for the peak months, the number is recorded to the side of the point on the graph. Total catch of each species for each year is also reported on each graph.

Index of Fishing Intensity

The only index of fishing intensity which could be devised is a relative one. It is based upon a tally of the cars (Fig. 2) paying tolls to and from Port Aransas via the Port

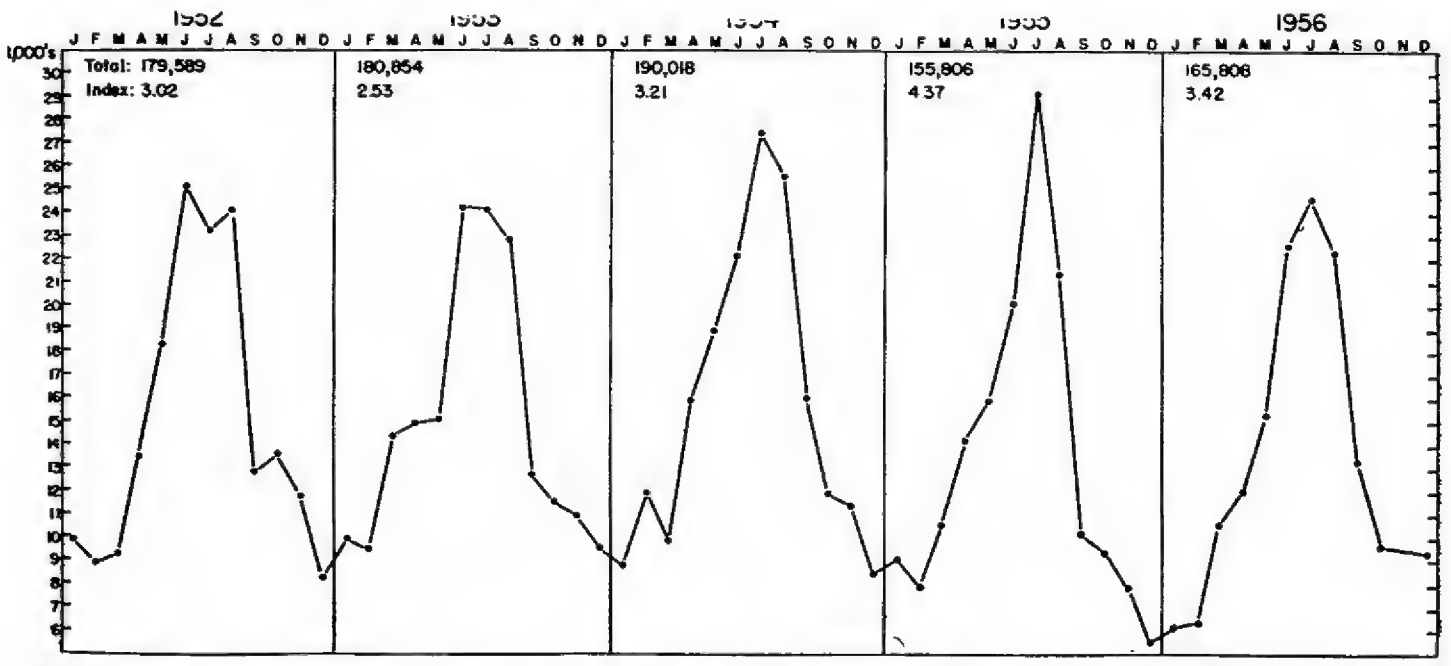
1952
1953
1954
1955
1956
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
1,000's
Total: 179,589
Index: 3.02
180,854
2.53
190,018
3.21
155,806
4.37
165,806
3.42

FIG. 2. Number of vehicles paying tolls to and from Port Aransas. Index equals number of times highest traffic month exceeds the lowest.

Aransas Causeway. This tally is maintained by the Nueces County Road District. No distinction is made between the number of cars entering or leaving Port Aransas, but presumably by halving the numbers for any date (to account for round trips), one would approximate the number of individual cars making trips for that date.

The index has a number of intrinsic faults. It is necessary to assume that the porportion of fishermen to non-fishermen remains constant throughout the year. This is obviously

incorrect since the ratio of fishermen would be considerably higher in the winter when sunbathing and swimming activities are almost non-existent. In addition, it assumes that a constant proportion of the occupants of the vehicles will proceed to and remain in the Port Aransas area. It is well known that some fishermen concentrate their activities on the causeway itself and others on the nearly twenty miles of beach between Port Aransas and Corpus Christi. A final difficulty is encountered when one considers the years 1955 and 1956. On November 9, 1954, the Padre Island Causeway opened a paved road from Corpus Christi to Port Aransas. This shunted many vehicles away from the Aransas Pass Causeway, which until that time was the major access to Mustang Island. The decrease in number of automobiles crossing to Port Aransas in 1955 and 1956 has been attributed by causeway authorities to bad fishing. This may be true as the proportionate change in the number of vehicles is not sufficient to account for the proportionately fewer fishes caught during 1955 and 1956. During the years covered in this study the number of vehicles using the Padre Island Causeway has steadily increased. There is no way of knowing if the number of cars entering Port Aransas via the Padre Island Causeway has increased at the same rate.

The graph of fishing intensity is reported as thousands of automobiles. The total number of cars for the year is given at the top of each year's record. Below this is listed an index which represents the number of times the heaviest traffic month of the year exceeds the least traffic month. The largest index (4.37, July and December, 1955) is not sufficient to account for differences in the peaks for the various species. Under the circumstances it was decided not to correct each month's catches using a monthly index based on the most active month, but to report the raw data unchanged and interpret it directly. We believe that the annual recurrences of largest catch peaks, bimodalities, etc. as seen on the graphs, are actual indications of abundance.

Fishing Tournaments

Every year during the second week in July, and for the past three years during the second week in October, fishing tournaments have been held in Port Aransas. These include private and charterboats. The only manifestation of these periods of increased fishing intensity, as indicated by the graphs, are found in the catches of sailfish and perhaps tarpon. Other than for these two species it is not felt that increased fishing during the tournaments influenced the catches of the other forms reported here.

Small Craft Warnings

A list of dates during which small craft warnings were raised nearby, at Rockport, Texas, are given below. These warnings affect offshore catches for the periods of their duration. However, since most offshore fishing occurs during the summer and most small craft warnings occur during the winter, it is doubtful that the charterboat catches reported here would be affected. In more violent periods jetty fishing is also affected by bad weather, and correlations can sometimes be made between periods of bad catches on the graphs and periods of bad weather as indicated in the list.

1952. January 9, 10, 22, 23, 27, 28; February 1–6, 13–16, 20, 24–26, 29; March 3, 9, 10, 12, 14, 15, 17, 18, 21, 22, 27, 28; April 1–4, 9, 10, 12, 22, 23; May 9, 17–19, 23–25, 27, 28; June 5; (Data missing for July, August, September and October) November 2, 9, 10, 18, 22–26; December 4, 9, 21, 22, 30, 31.

1953. January 1, 2, 8, 9, 11, 12, 14–17, 20, 22–24, 27, 28, 31; February 1, 2–6, 8–11, 14–17, 19, 20; March 1–4, 12–14, 21–23, 29–31; April 5, 6, 12, 15–18, 23–25, 28–30; May 4, 10, 12, 13, 18, 19; June, July, August, September: none; October 26; November 7, 8, 19, 22, 24, 25; December 2, 3, 5, 6, 8, 9, 11–14, 21–23, 27–30.

1954. January 8–16, 20–22, 30, 31; February 6, 7, 10, 11, 15, 16, 18–20, 23, 25–28; March 1–3, 11–13, 17–19, 31; April 1, 7, 8, 15, 16, 29, 30; May 1, 2, 11, 12; June 25, 26; July 2, 3; August: none; September 10–12, 16, 17, 21, 22, 30; October 1, 3–7, 14, 15, 22, 23, 26–30; November 2–4, 10–15; 17, 18, 23, 24, 26–28; December 4–6, 8, 9, 11–17, 27–29.

1955. January 5, 6, 12–15, 17, 18, 20, 21, 23, 24, 27, 28; February 3–5, 9–11, 17–21, 26, 27; March 5, 6, 16, 17, 20, 22, 25–27, 31; April 1, 3, 4, 6, 7, 12, 13, 23; May 7, 8, 11, 12, 25, 26, 28, 29; June 8, 9, 21, 22; July 13, 14, 31; August 1; September 4–7, 11–14, 17–19, 28–29; October 6, 7, 12–14, 16, 17, 23, 24, 28, 29; November 2, 3, 5, 8, 11, 12, 15, 16, 22, 23, 27, 28; December 3, 4, 8, 11, 12, 14–16, 30.

1956. January 7, 17, 18, 29, 30; February 1–13, 17, 18, 25, 27; March 3, 6–8, 10–13, 21, 22, 27, 28; April 2, 3, 5–7, 9, 10, 14, 15; May 2, 3, 15, 31; June 1; July 26, 27; August: none; September 6, 7, 10–12, 22, 23, 30; October 18, 20, 21, 25, 26, 30; November: data missing; December 8, 9, 12, 13, 17, 18, 22, 23.

Discussion of the Species

The Tourist Bureau reports list the fishes by their common names. Most of these names are ascribable to particular species, others are not [*i.e.* shark, flounder, bonito (includes *Euthynnus alletteratus* and *Sarda sarda*), whiting (includes *Menticirrus littoralis* and *M. americanus*), grouper, trout (may include *Cynoscion arenarius*, *C. nothus*, and occasionally *C. nebulosus*)]. For recognizable fish both the common and scientific names are included in this paper; the unidentified fish are not discussed.

Tarpon—*Megalops atlantica* (Fig. 3)

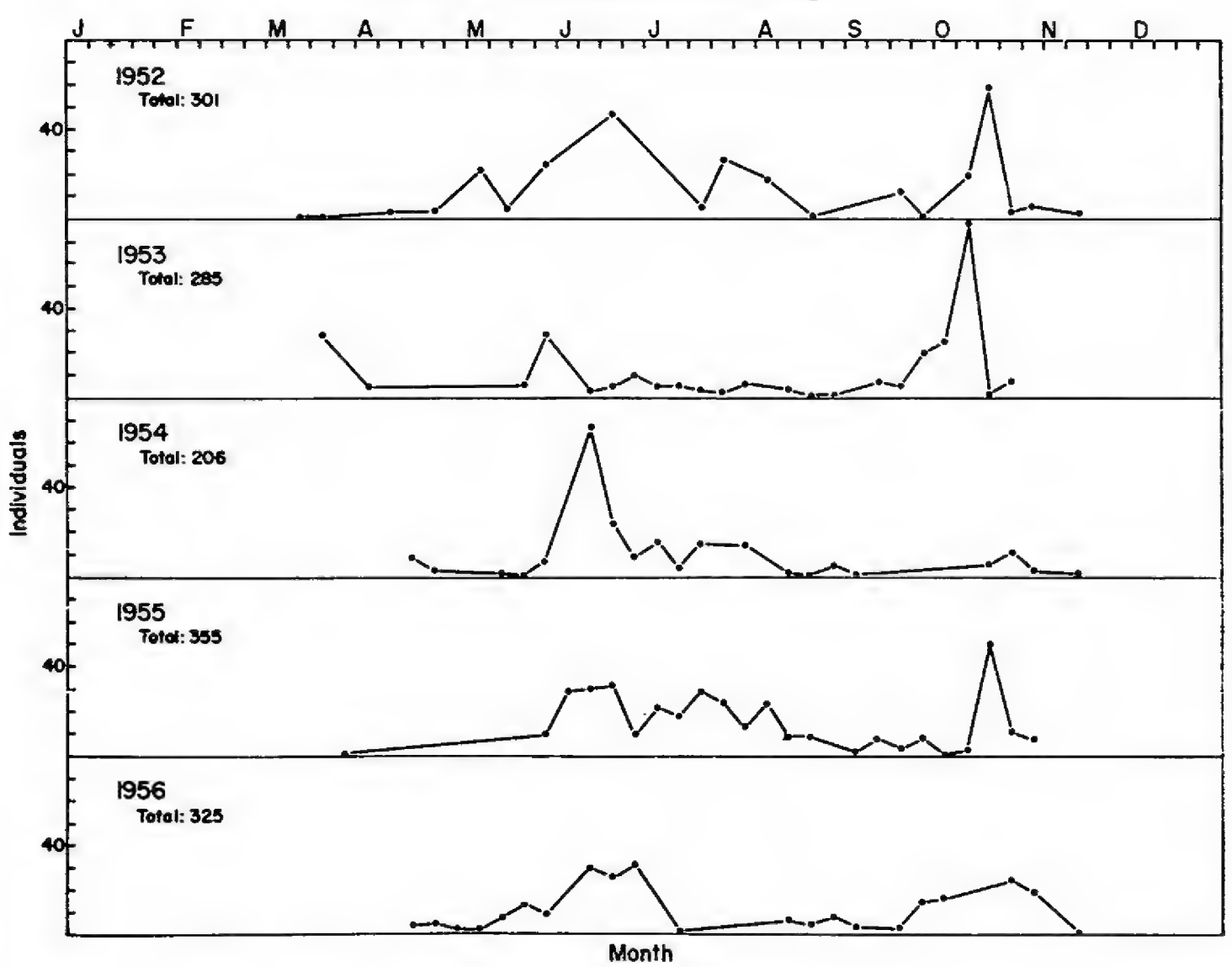

FIG. 3. Tarpon.

Some of the game fishes which are included in the reports are not discussed here because they are caught or reported only sporadically. These fishes include white and blue marlin, barracuda, amberjack, junefish, wahoo, ladyfish, spadefish, and gafftop catfish.

Tarpon are primarily caught in the summer and fall. The graph indicates that there is a bimodal peak each year: one in June and one in October. Mr. Terry Leary, of the Texas Game and Fish Commission, informs me that the tarpon are in the bays during the summer, and Gunter (1945) reports two specimens taken in late July and late September from Copano Bay. Peaks would be expected for Gulf catches when the tarpon are entering and leaving the bays. Whether or not tarpon enter or leave the bays to spawn is not known. It may be that the peaks are artifacts associated with the fishing tournaments, but if such were the case, no recognizable peaks would be found during 1952 and 1953 when October tournaments were not held.

From November or December through March there are no records of catches. Presumably the tarpon are in the warmer offshore waters. Farrington (1949) notes that the tarpon arrive off Port Aransas in April and remain until November, and lists the best fishing months as May through October.

Sailfish—*Istiophorus americanus* (Fig. 4)

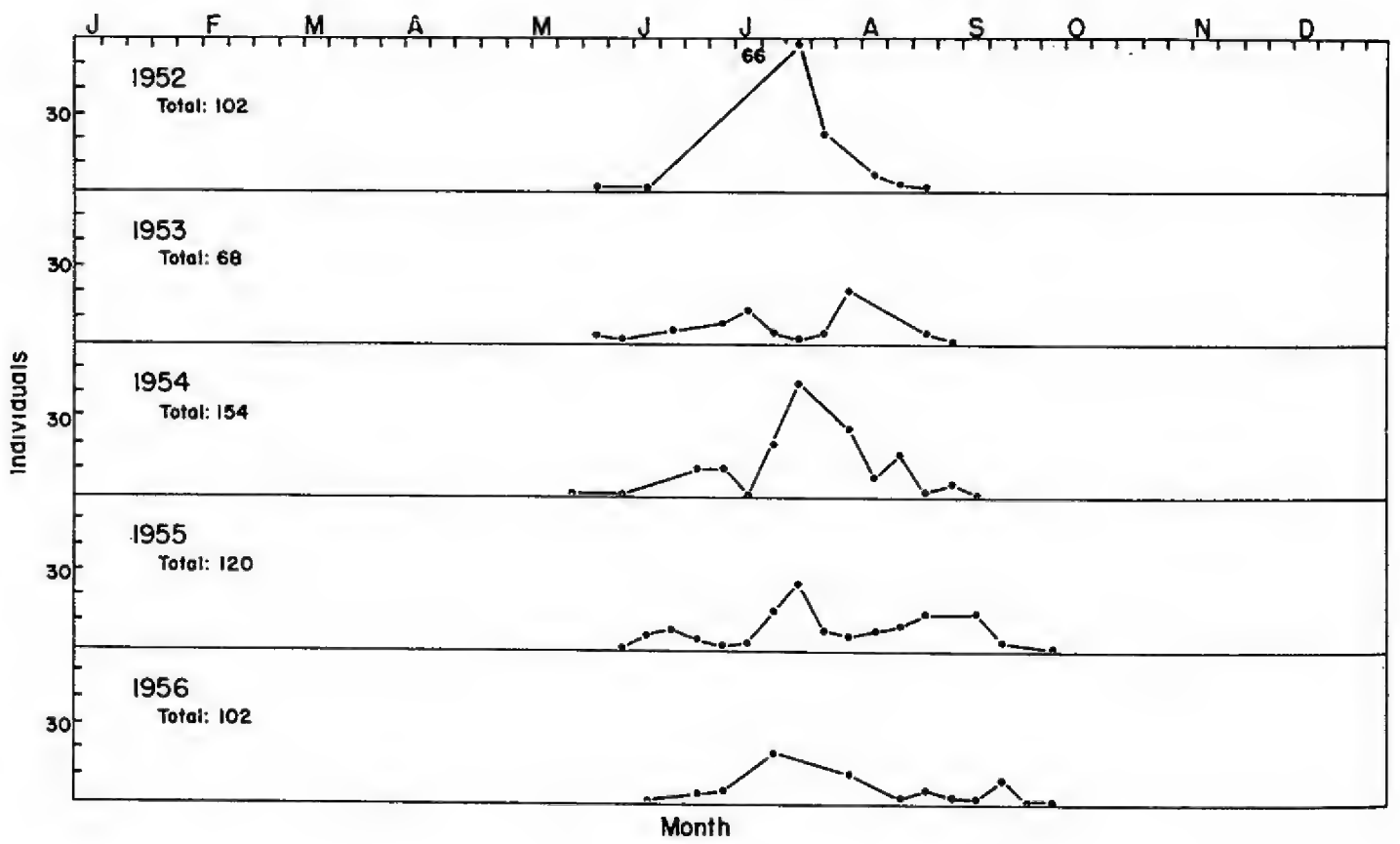

FIG. 4. Sailfish.

Sailfish are caught only from late May through September. Baughman (1954a) states that sailfish appear off the Freeport-Galveston area as early as May 2. Peak months are usually July and sometimes August. The peaks seem to be associated with the July fishing tournaments, although they may be the result of spawning and associated concentrations. Gehringer (1956) reports larval sailfish in the western Gulf from June, and spawning possibly occurs through August (Baughman 1941a).

Commercial fishermen and charterboat men have informed us that sailfish are often seen in schools at the snapper banks, approximately forty miles offshore, during the wintertime. Summer fishing for sailfish takes place as close as six miles offshore. It is

the opinion of the charterboat men that these fish could be caught year round, but that no one has made an effort to do so, most likely because of the increased expense of traveling further out to sea and because of the less predictable winter weather.

It is quite possible that there is a potential winter sport fishery in the area which could, with proper advertising, result in increased revenue for the area.

Spanish Mackerel—*Scomberomorus maculatus* (Fig. 5)

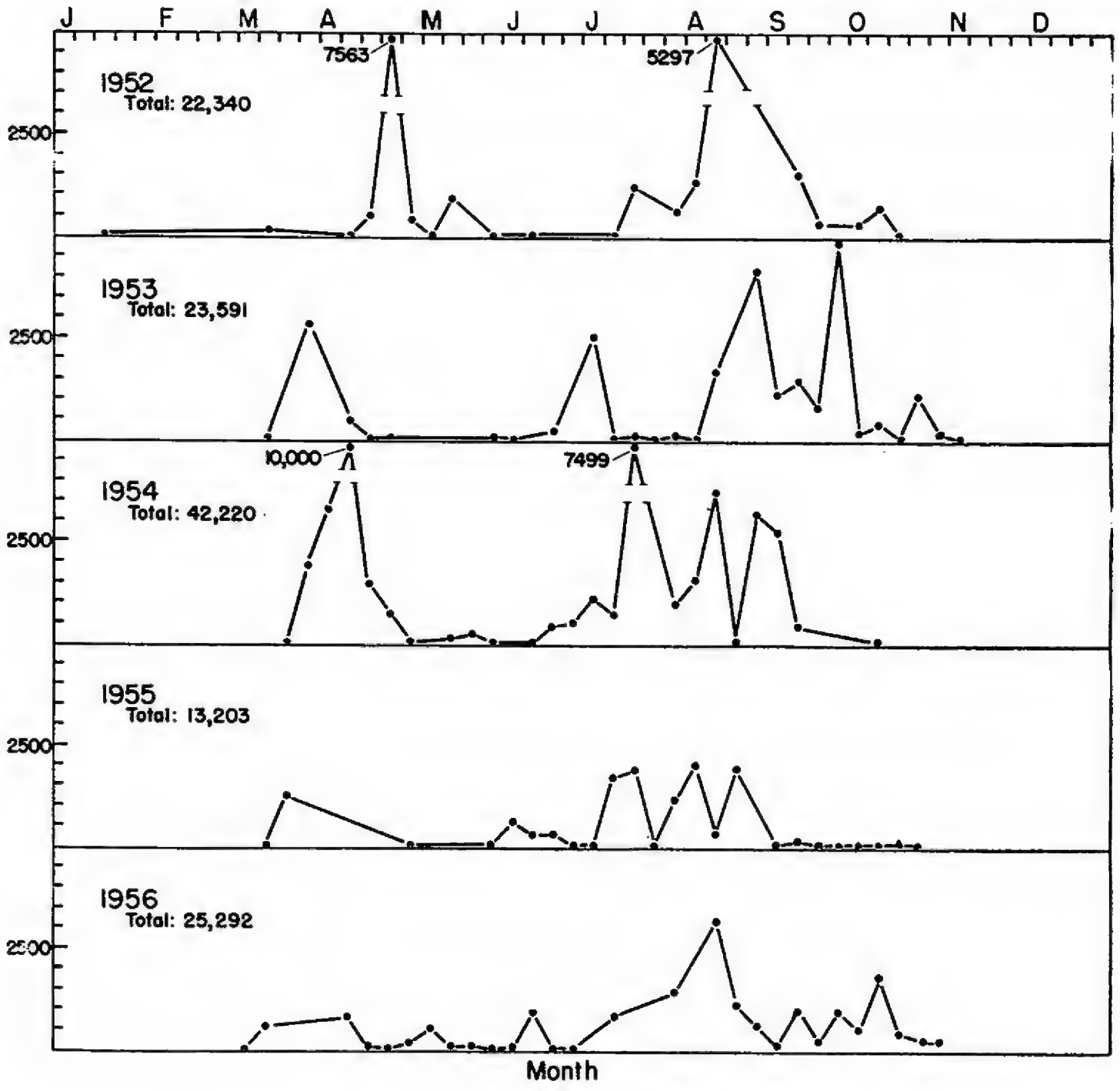

FIG. 5. Spanish Mackerel.

Spanish mackerel are most frequently caught during the months from March through October. The times of peak months vary, but there appears to be a bimodality with the greatest catches occurring in March and April and again in July, August, and September. Gunter (1945) states that some mackerel (about 11 percent of his catches) enter the bays in the summer, and it is possible that the phenomenon here may be the same as indicated for the tarpon. Gunter also noted that the greatest commercial catches were made on the Texas coast during August. He states that the only month during which mackerel were not taken was February. Although not graphed here, mackerel were being caught during the week of February 19 to 26, 1957.

LaMonte (1951) reports that this species is common off Florida from November through March; the months when this species is least common off the Texas coast. This might indicate a migration occurring from one side of the Gulf of Mexico to the other.

Kingfish—*Scomberomorus cavalla* (Fig. 6)

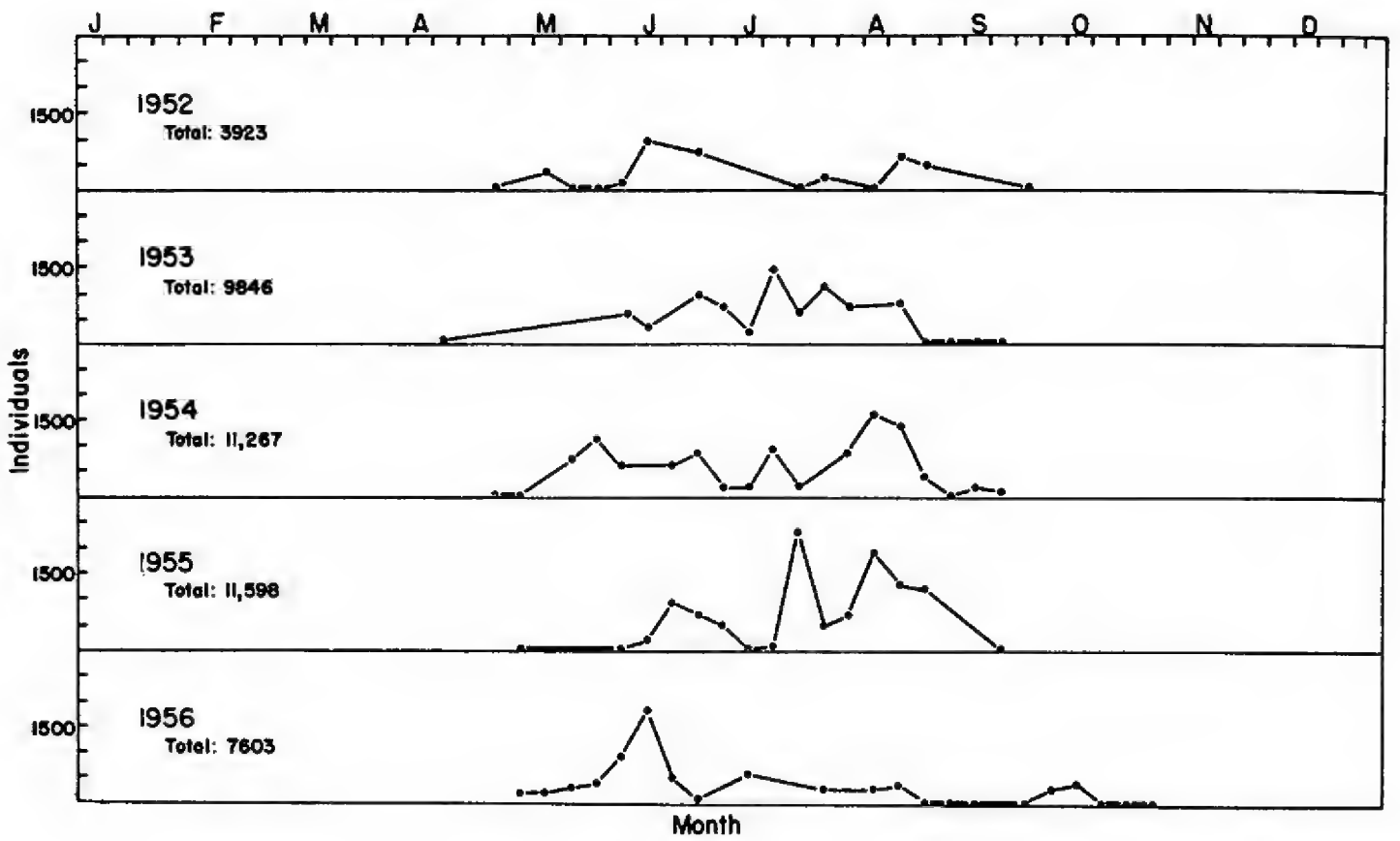

FIG. 6. Kingfish.

The kingfish is taken primarily in the summertime. It is possible that this also is an example of lack of fishing intensity during the winter months. These fish, like the sailfish and dolphin, are caught only from the charterboats and private boats.

Rivas (1951) reports that this species is most common around south Florida during the winter months, which may indicate a migration around the Gulf similar to that suggested for the Spanish mackerel.

Dolphin are caught almost exclusively during the summer months, showing very sharp peaks during the month of August, although the 1956 peak occurred in May (this has not been repeated in 1957). Sharp peaks such as these may indicate migrations, wherein fish are present in large numbers for short periods of time while they pass a point. Baughman (1941b) reported a large run of dolphin which passed by Freeport during the last week of May, 1939.

LaMonte (1951) states that dolphin are, in general, present from June through October on the eastern seaboard. She also states that young are plentiful around Beaufort in late summer. We have collected several young from drifting seaweed *(Sargassum)* in the Lydia Ann Channel during July, 1957, and Pew (1957) reports collecting young from Aransas Bay during the months of April, May, August, and October (ranging from 32 to 55 mm.).

The common jack is caught from February or March through October and sometimes November. Peak months are variable, occurring in March, May, June, and October.

Gunter (1945) collected most of his specimens from the bays during August. All these were young of less than 60 mm. which may indicate that the bays serve as nurseries for this species.

Dolphin—*Coryphaena hippurus* (Fig. 7)

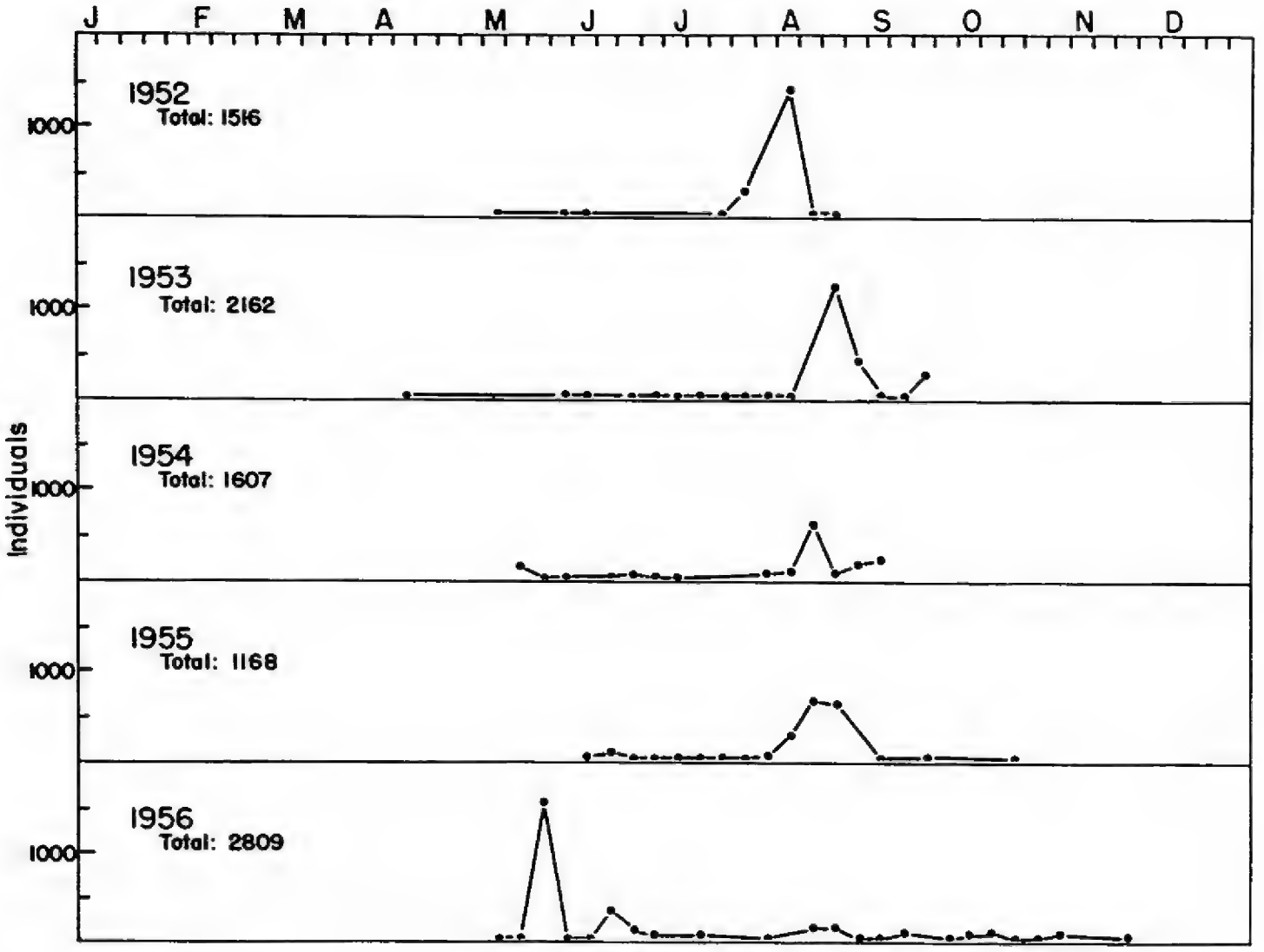

FIG. 7. Dolphin.

Jack Crevalle—*Caranx hippos* (Fig. 8)

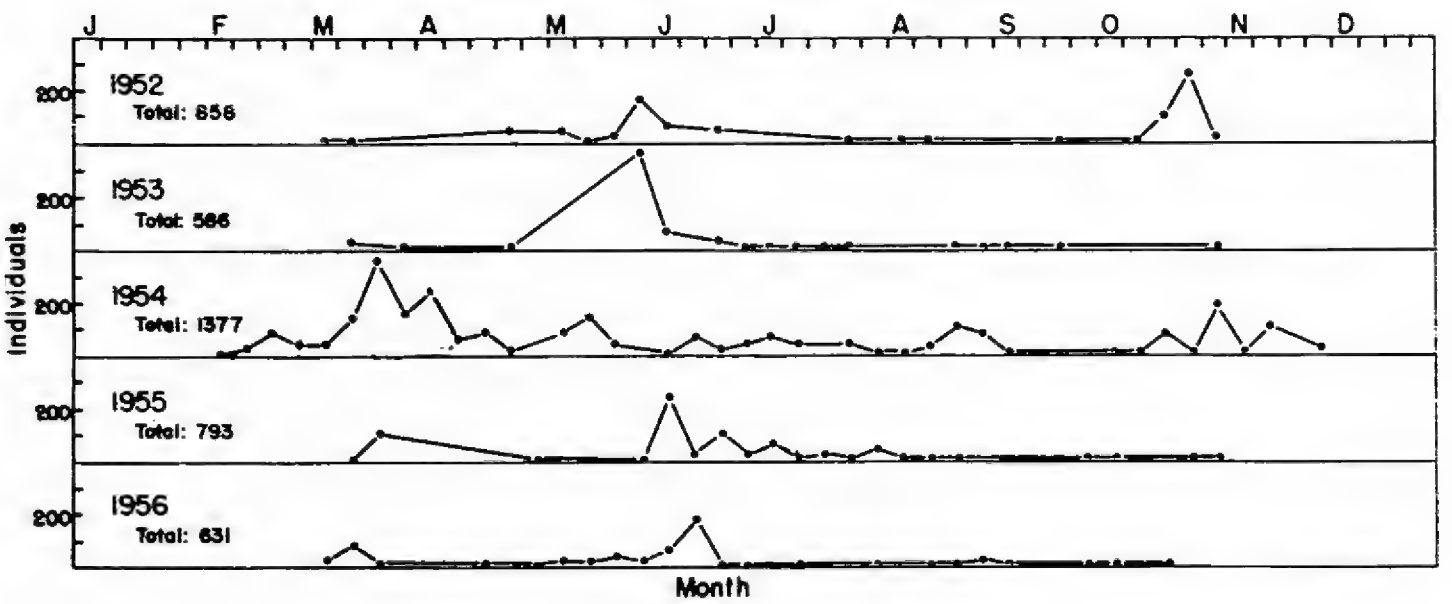

FIG. 8. Jack Crevalle.

Pompano are caught all year long, but major catches occur during March, April, and May. These months are probably just prior to the breeding period as Gunter (1945) reports young as small as 13 mm. from June, and states that fish as small as 23 mm. were taken from June through December. He also notes that this species is taken all year by commercial fishermen on the coast, but to a lesser extent during the winter. Simmons (1957) reports that large schools of pompano were present in Laguna Madre during the months of September and October.

Pompano—*Trachinotus carolinus* (Fig. 9)

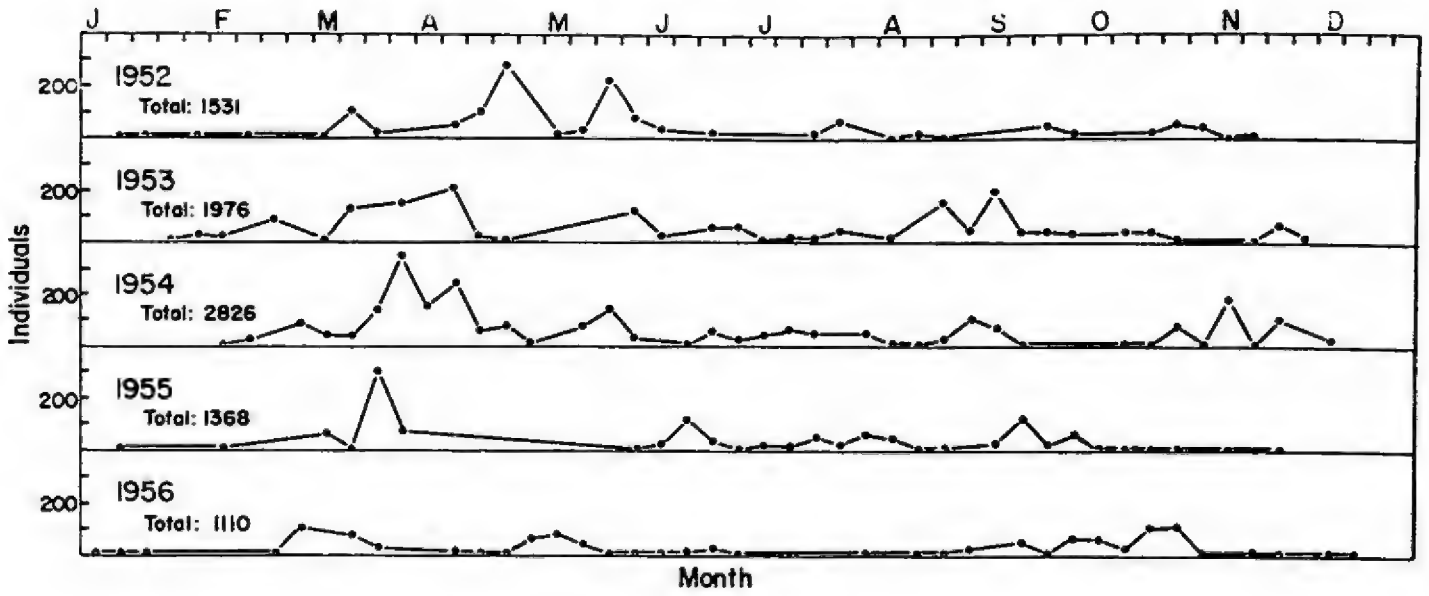

FIG. 9. Pompano.

Bluefish—*Pomatomus saltatrix* (Fig. 10)

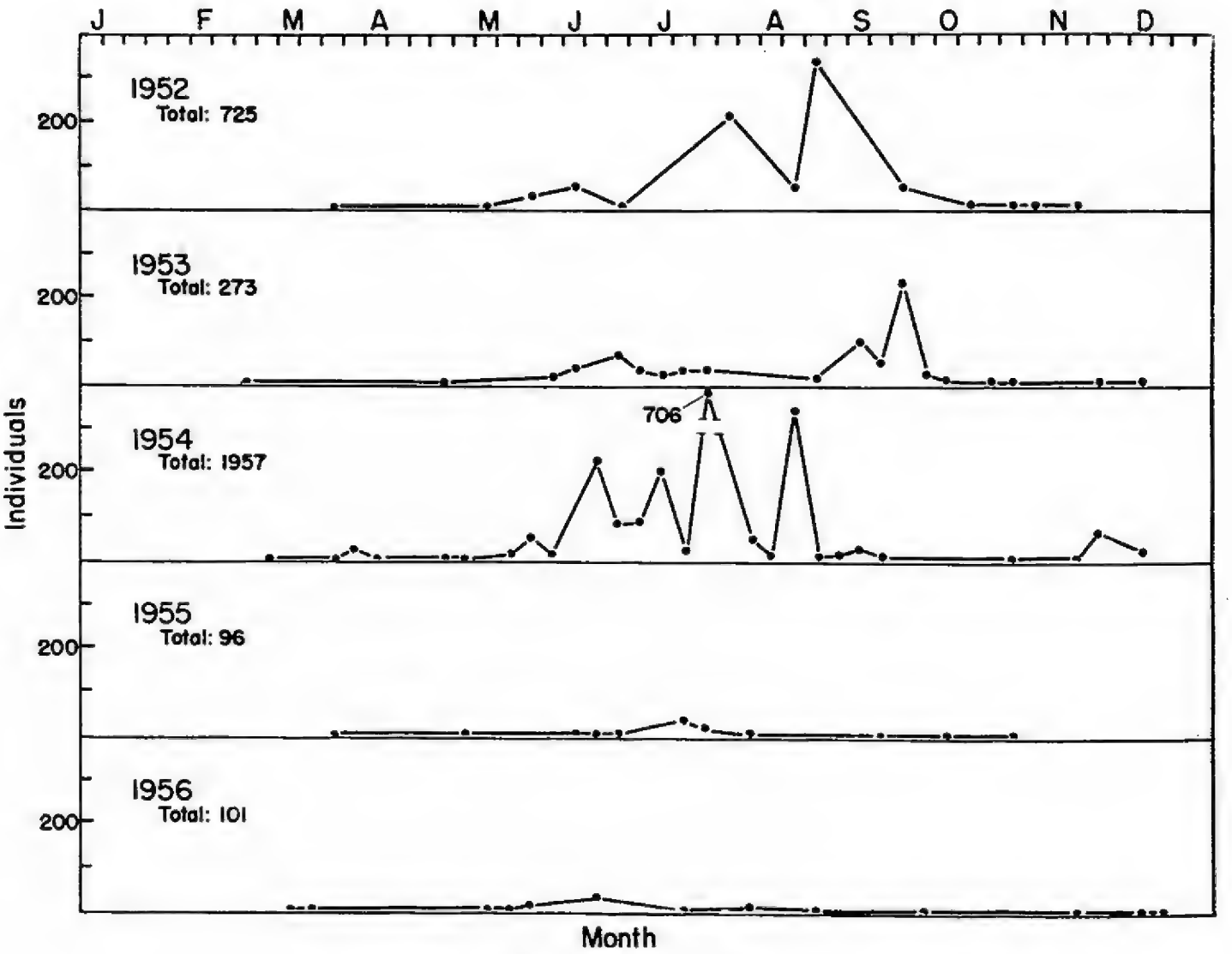

FIG. 10. Bluefish.

Bluefish are caught primarily from March through September, and appear to be entirely absent during December and January. The peak months are July and August. Catches are variable from year to year, but during 1955 and 1956 they fell off markedly. Gunter (1945) noted an absence of this species during the years 1936–1942, exclusive of 1937–1938, during which time 395 pounds were reported from the Texas commercial landings.

Bigelow and Schroeder (1953) give interesting data on the bluefish off the northeastern coast of the United States, but state that little is known about Gulf of Mexico populations. Ripe individuals are taken off Chesapeake Bay during late spring and summer, and catches are low or absent during the winter in that area. However, some commercial catches are made off Key West, Florida during the winter.

Cobia—*Rachycentron canadus* (Fig. 11)

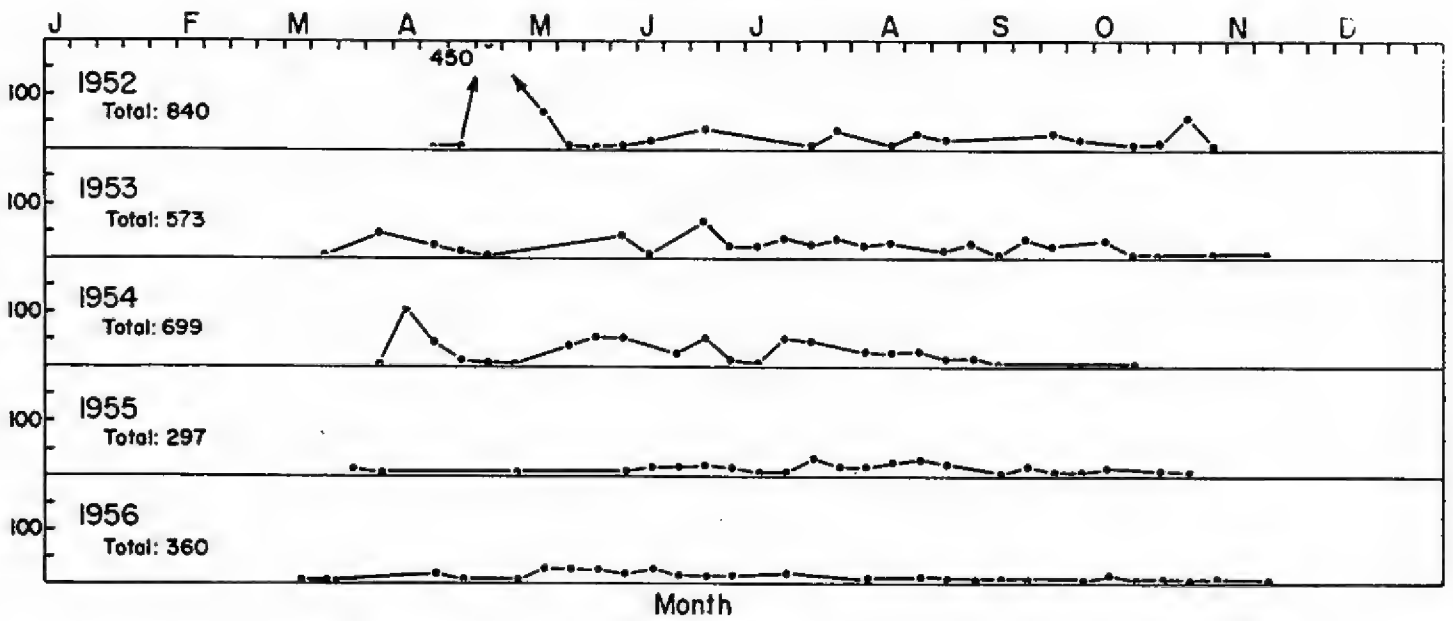

FIG. 11. Cobia.

Snook—*Centropomus undecimalis* (Fig. 12)

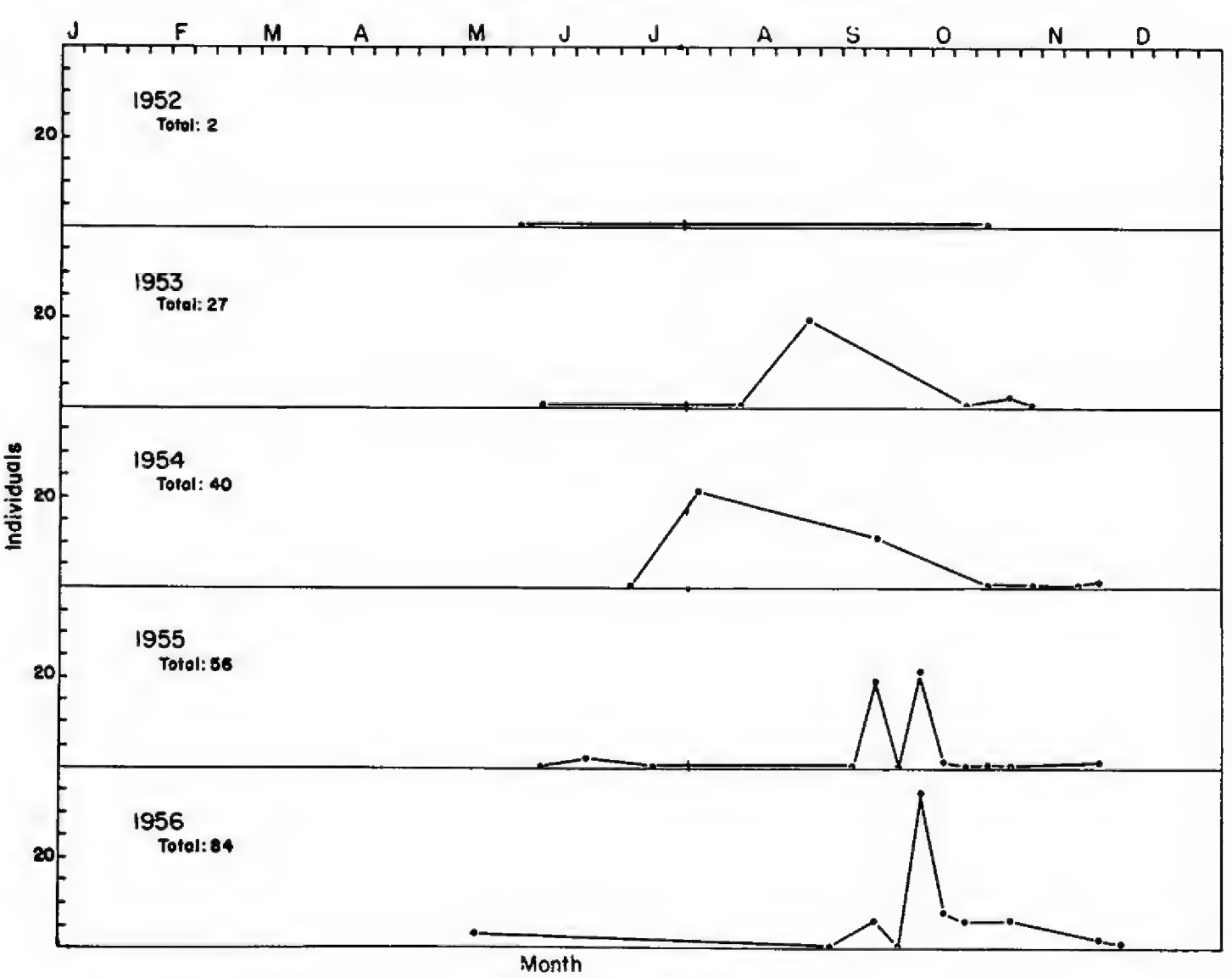

FIG. 12. Snook.

Cobia are caught from February or March through October or November. Only during April, 1952, did there appear to be a recognizable peak. Although not fished for specifically, cobia are esteemed as a food fish.

Snook are caught infrequently at Port Aransas. The best months appear to be from mid-July until late September. Nothing is known of the spawning habits of the snook in this region.

Mangrove Snapper—*Lutjanus griseus* (Fig. 13)

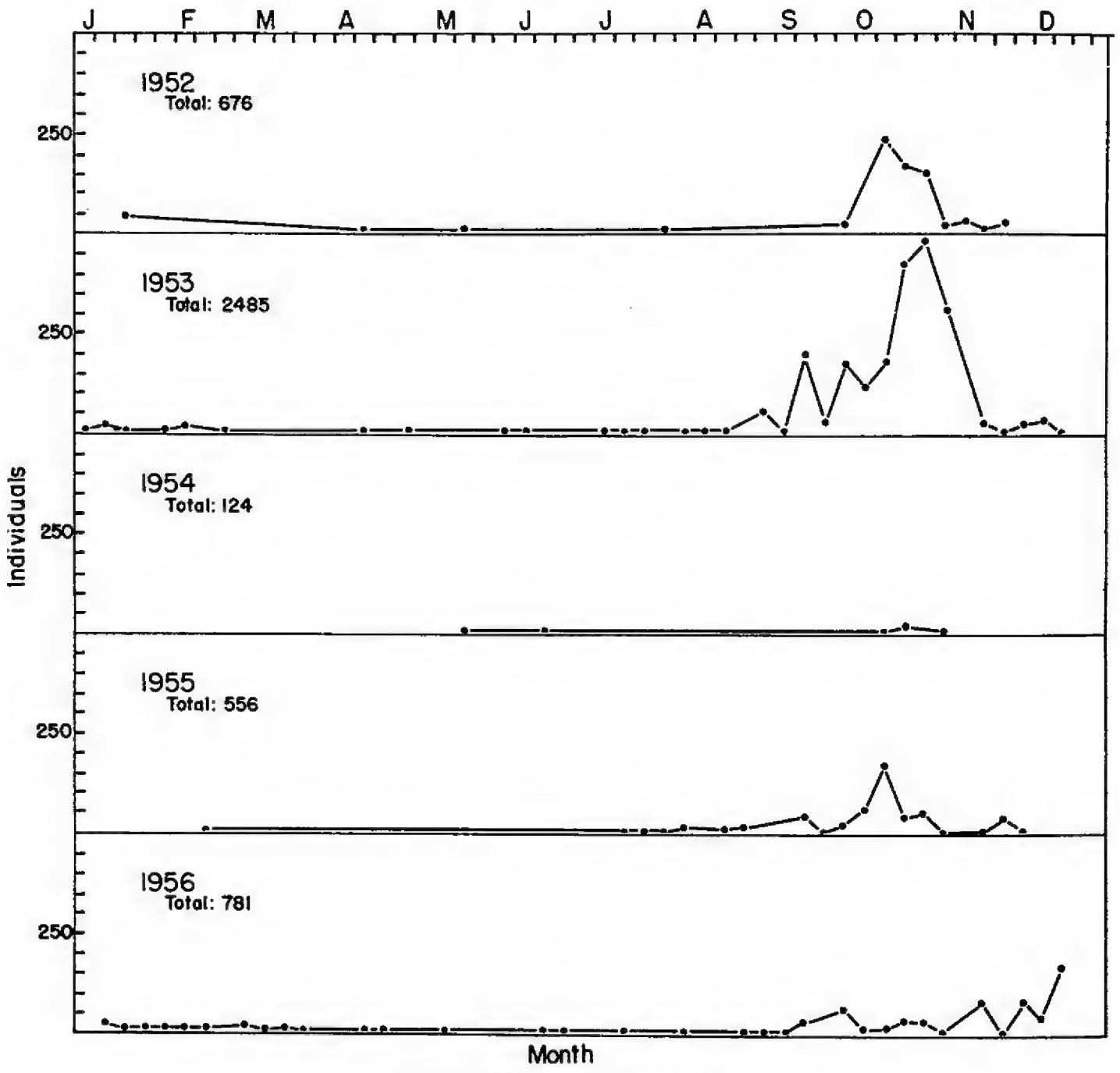

FIG. 13. Mangrove Snapper.

Mangrove snapper are caught throughout the year. The catches are quite variable from year to year, but the peak month is most often found in October and is sharply defined. Information concerning the breeding habits of this species is not available.

Spotted sea trout are caught throughout the year, but the best months are May through July, and secondarily, October and November. Catches appeared to be very low during 1956, but this may be the result of tabulation. Catches were frequently reported simply as "trout" during the latter part of 1956 and were not graphed, but they may have been partly ascribable to this species.

Gunter (1945) found peak catches for this species during the winter in Copano and

Spotted Sea Trout—*Cynoscion nebulosus* (Fig. 14)

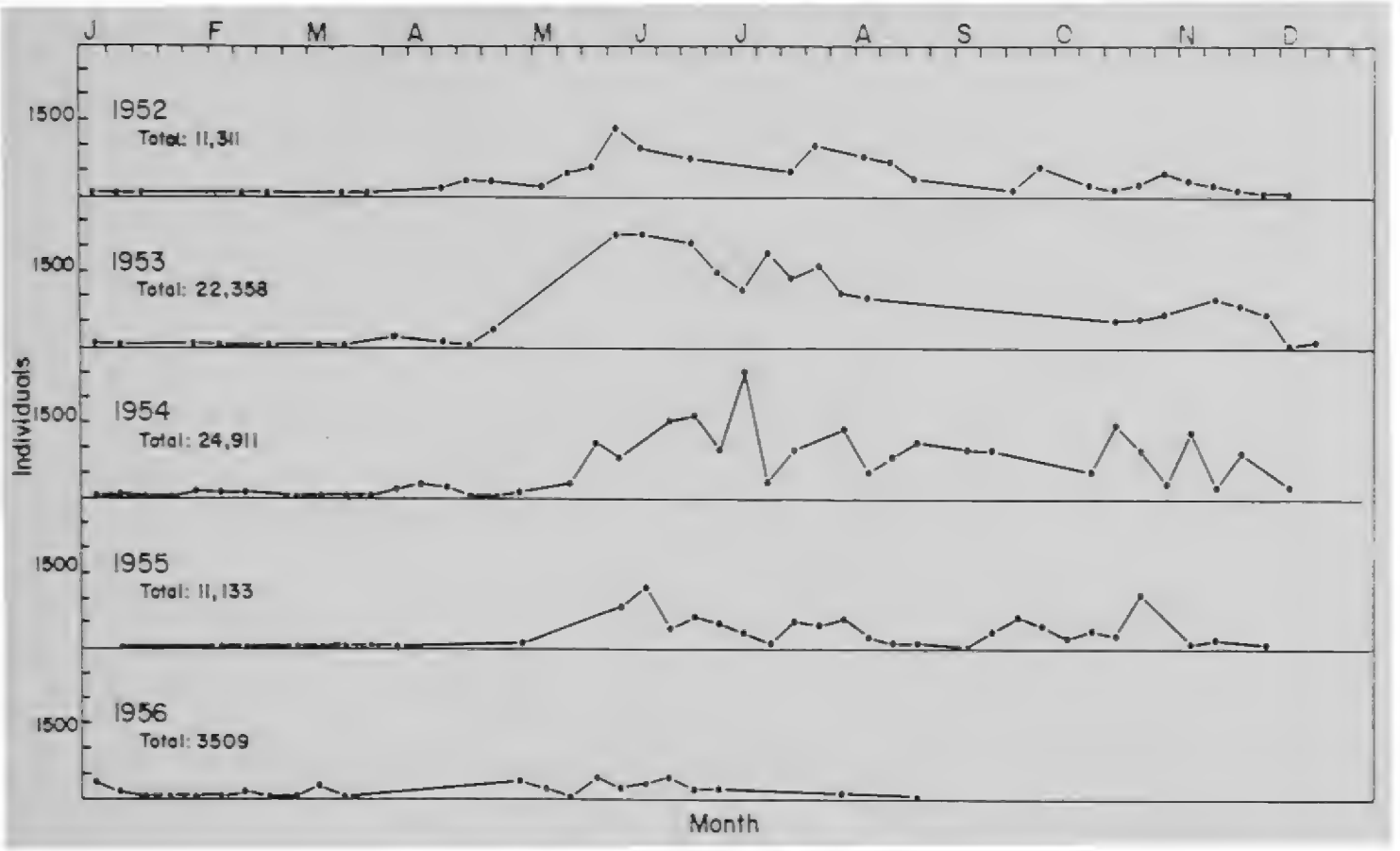

Fig. 14. Spotted Sea Trout.

Aransas bays. Ripe fish were found from April through November. Simmons (1957) found small trout common in Laguna Madre in April, May, and October. According to Pearson (1928) spotted trout spawn in the bays from early spring through October, with the height of the season during April and May.

Drum are caught throughout the year. The best catches are usually made from October through February, and the highest peak occurs in November of each year. Gunter (1945) found October through April to be the peak months for the years 1941 and 1942. He also pointed out that the fall and winter months provide the greatest catches of this species in the commercial fishery of the Texas coast.

Pearson (1928) states that from February until May the drum are spawning. Large migrations take place from the bays to the Gulf. He also states that a secondary spawning sometimes occurs from July through November. Sport catches for 1953 and 1954 would indicate such a secondary migration into the Gulf.

Although croaker are caught during most of the year, there is no month which can compare with the October–November peaks. Pearson (1928) reports that ripe adults migrate from the bays to the Gulf during September and October; spawning takes place from October to February. Suttkus (1955) found that croakers migrate out of Lake Pontchartrain, Louisiana, during September, October, and November, associated with the decrease in water temperature. First young of the spawning were caught in the lake during November. It was found that most of the fish did not exceed two years in age (also Pearson, *op. cit.*, for Texas). On the basis of the above information the single peak period at Port Aransas might be explained by the migration into the Gulf of the previously spawned fish which had migrated into the bays as small individuals, too small to be caught.

Texas Game and Fish Commission yearly reports show that croaker are frequently absent from the commercial fishery (which is in the Gulf) during the spring and summer.

Drum—*Pogonias cromis* (Fig. 15)

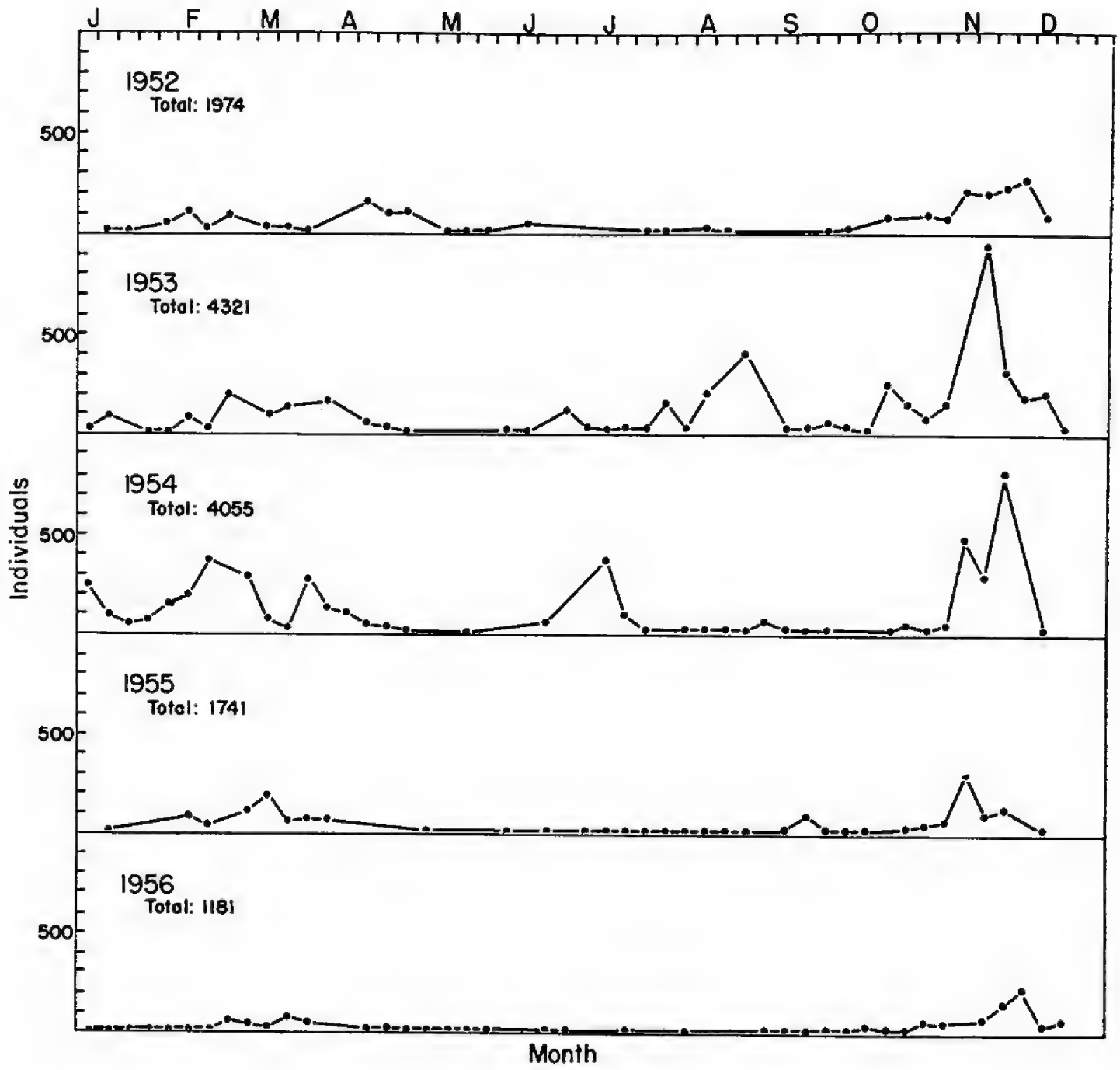

Fig. 15. Drum.

Croaker—*Micropogon undulatus* (Fig. 16)

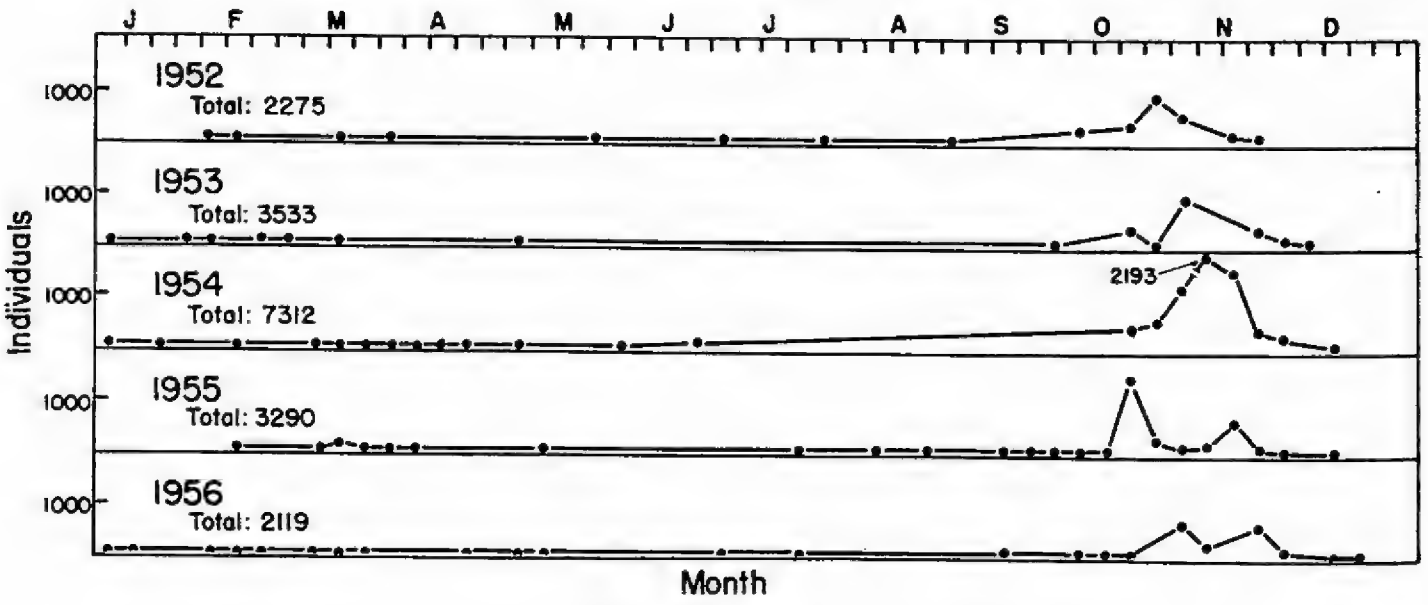

Fig. 16. Croaker.

and also that the peak month is most commonly October. In collections from Texas bays, Gunter (1945) reported the largest catches of croaker during the spring and summer months.

Redfish (Channel Bass)—*Sciaenops ocellata* (Fig. 17)

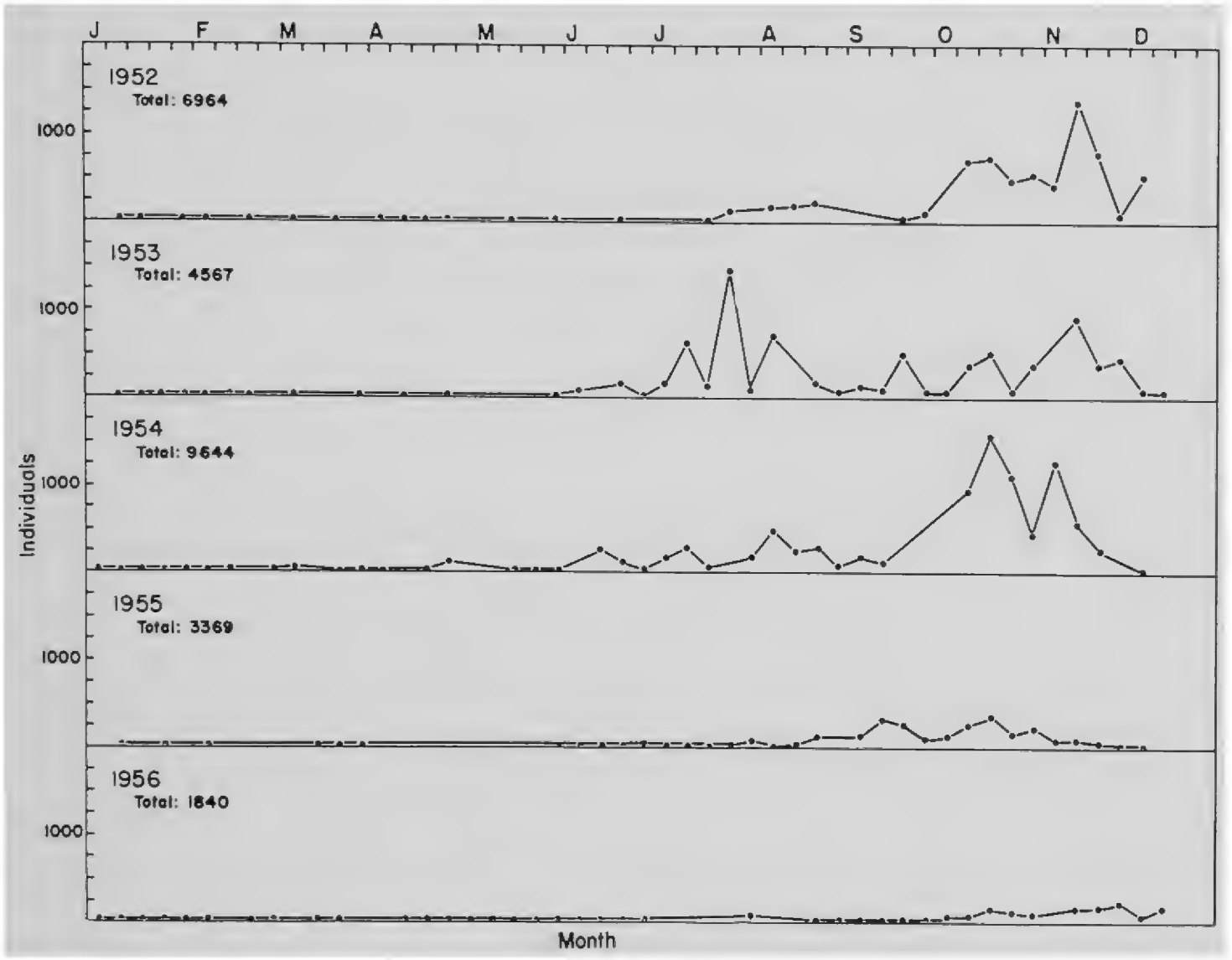

FIG. 17. Redfish.

Redfish are caught throughout the year, but the peak months usually occur in the fall when the adults are leaving the bays to spawn in the Gulf (Pearson, 1928). Sometimes, however, large catches occur in July and August. A notable decline was observed during 1955 and 1956.

Sheepshead are caught all year, but the best months are from October to February. These findings agree with Farrington's (1949) report and also with tabulations of the commercial catch for the Texas coast, as reported in the yearly reports of the Game and Fish Commission. An additional high for the month of July, 1956, is reported by the Game and Fish Commission for the commercial fishery, but this does not show on the Port Aransas records.

Conclusions and Summary

The Port Aransas sport fishery is an open Gulf and channel mouth fishery, as opposed to numerous bay sport fisheries in the area. Open Gulf fishing takes place from charter-boats and piers, and the channel mouth fishing takes place from the jetties. The types of

Sheepshead—*Archosargus probatocephalus* (Fig. 18)

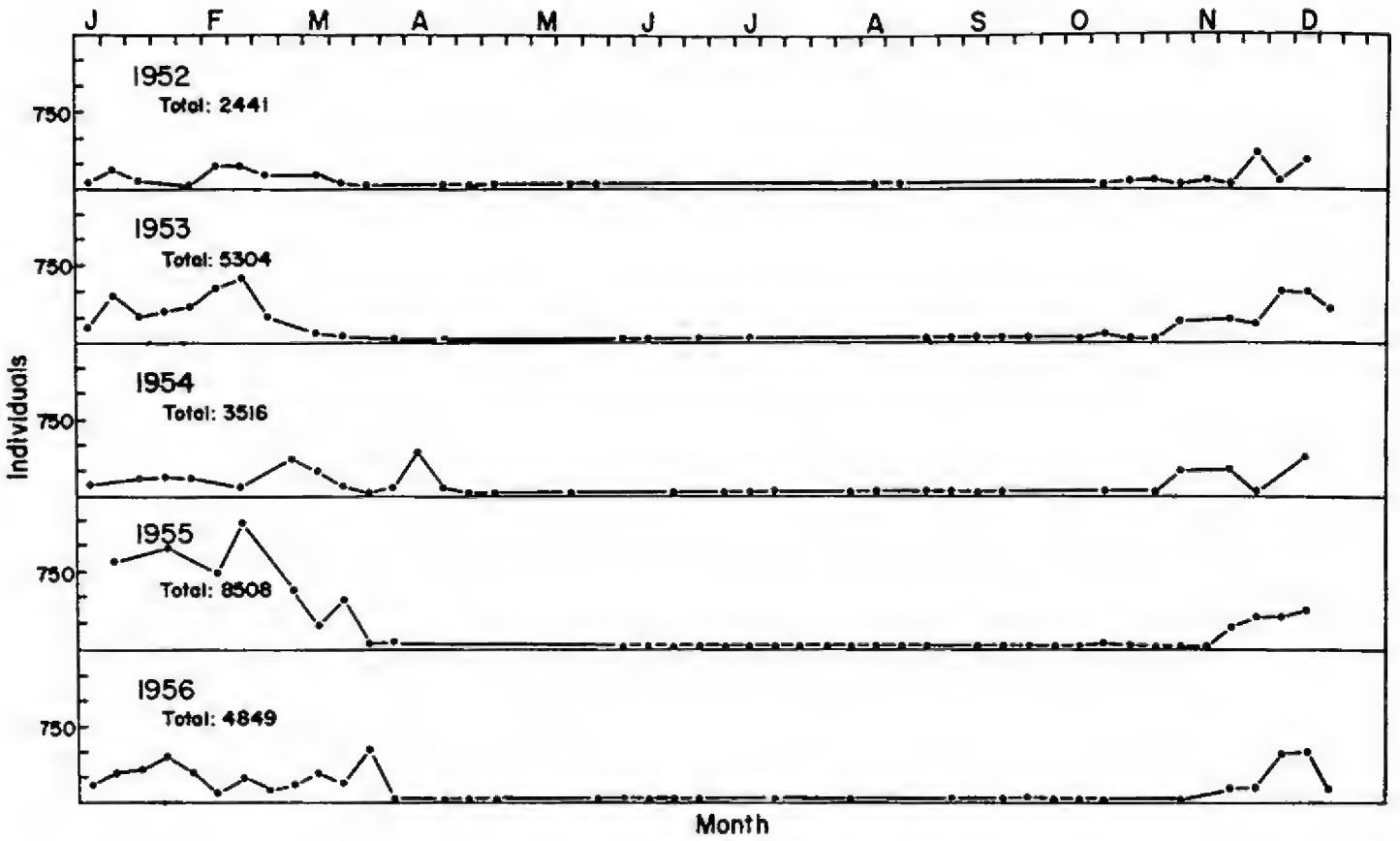

FIG. 18. Sheepshead.

fishes caught from the charterboats (sailfish, kingfish, dolphin, cobia, etc.) differ from those caught from the jetties and piers (redfish, mangrove snapper, drum, croaker, sheepshead, etc.); however, tarpon are taken from all three places. Fishing from charterboats takes place almost exclusively during the summer although it appears that the fishes caught may be present in the area all year. Fishing from the piers and jetties occurs all year long with certain fishes providing peak catches during various times of the year; however, most of the species recorded here provide fall or winter peaks for fishing. On the basis of life history studies in the literature (particularly for the sciaenids) the Port Aransas jetty and pier fishing is dependent upon the fact that certain species leave the bays and enter the Gulf to spawn. They exit at Port Aransas through the only channel (Lydia Ann) for approximately sixty miles to the north and one hundred thirty miles to the south.

In view of the recent interest in the cutting of fish passes to the north and south of Port Aransas, it should be pointed out here that there is a possibility such passes will diminish the catches of the migrating bay species at Port Aransas. This effect could be accomplished by diverting the fishes which would ordinarily exit at Port Aransas. The cutting of passes may also diminish total fish caught if sports fishing does not take place at points in the vicinity of the Gulf openings of the passes. Whether or not the opening of passes will allow the bay species to increase in number in the future and offset the diverting effect is a matter of less predictable nature.

There has been a considerable drop in the number of fish caught for several of the species discussed herein during the years 1955 and 1956, as compared with 1952–1954. The causes for the decreases are manifold, and we do not feel the information available is sufficient to explain them.

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Population Studies of the Shallow Water Fishes of an Outer Beach in South Texas

GORDON GUNTER

Gulf Coast Research Laboratory
Ocean Springs, Mississippi

Introduction

The vertebrate life of the beach environment is little known. Pearse, Humm, and Wharton (1942) reported the fishes and invertebrates taken in 68 seine hauls on inside and outside beaches near Beaufort, North Carolina. Gunter (1945) reported on 35 minnow seine and 23 beach seine hauls made monthly over a year and a half on the beach of Mustang Island, Texas. These are the only recent reports of seining studies of outside beaches from North America. Warfel and Merriman (1944) made a study of an inside beach on the east side of the harbor of New Haven, Connecticut. Several earlier reports of fishes collected in Atlantic waters, but compiled for other purposes, are cited by Warfel and Merriman. In this study hauls along the Gulf beach of Mustang Island were made during separate periods, totaling 10 months, in three different years.

The Institute of Marine Science of The University of Texas was headquarters for the work. Mr. David Kramer, who first began this work with the writer, collected most of the data. I am indebted to him and in part to Mrs. Kramer, who also assisted.

LOCALITY

Mustang Island is one of the barrier islands lying between the bays and the Gulf, which are typical along the Texas coast. It lies east of Corpus Christi Bay and is part of the western shore of the Gulf of Mexico. This island lies in the dry subhumid zone of Thornthwaite (cf. Collier and Hedgpeth, 1950). It is 16 miles long and runs almost due north and south, bearing a little to the east. The island and the general locality have been figured and described by Gunter (1945) and Collier and Hedgpeth (1950) and is also described in current geological papers. A map of this area is provided as Figure 1 by Hoese (1958) in this volume.

The beach itself has very gradual slope back to the sand dunes and is made up of fine sand. The offshore slope is gradual and approximately six sand bars lie parallel to each other to a distance of a quarter mile offshore.

In 1947, the southern end of the island was separated from Padre Island by a shallow pass, Corpus Christi Pass, into Corpus Christi Bay. However, Aransas Pass at the north end of the island is maintained at an artificial depth as ship channel, and the nearby passes will not stay open. Corpus Christi Pass closed in May, 1949, joining Padre and Mustang Islands. This abolished collection station number one, which was located inside Corpus Christi Pass.

The Mustang Island beach differs from those on the northern Gulf coast in two major respects. Large rivers do not occur nearby and there is usually very little driftwood on

the beach. Secondly, it is part of a very windy coast, the average wind speed at Corpus Christi being 11 m.p.h. Therefore, the surf is usually rough and the inshore water is often roiled and muddy. It is remarkable that so many delicate, young and juvenile fishes, as are found there in warmer months, can live in this surf.

Method

The seine used for collecting was fifty feet long and four feet deep and made of mesh measuring one quarter of an inch stretched. After the work was finished the meshes measured three to an inch, but whether stretching was slow or took place after the preliminary use is not known.

Eight stations were established. The first was a little less than one half mile inside Corpus Christi Pass, on the Mustang Island side, with the second at the mouth of the pass. The third was one mile north of the pass on the outer beach. Stations four, five and six were equally separated at about five-mile intervals going northward, the last within one mile of Aransas Pass. Station seven was at the angle made by the south jetty of this pass and the beach. The last station was a little more than one half mile inside the mouth of Aransas Pass. They were numbered one to eight starting at the inner Corpus Christi Pass station and ending at the inner Aransas Pass station.

At each station the seine was carried as far out as possible, then spread and pulled ashore. At the two pass stations, where the water was deeper close to shore, sweeps parallel to the shore were made.

The fishes captured were identified and measured in millimeters in the field. Air and water temperatures were taken by a mercury thermometer reading in tenths of a degree centigrade. The salinity at each station was determined by titration.

Results and Discussion

Temperature and Salinity

In Table 1 the water and air temperatures at each station are indicated. They show rather consistently the lag of water temperatures behind air temperatures when the seasons are changing. The temperatures for August, 1949 are close to the maximum for shallow open waters in this region, but the recorded temperatures for the cooler months do not approach the minimum since collections were not made in January through March.

In Table 2 the salinities at each station are given. The period 1948 to 1953 was very dry due to a long drought (cf. Parker, 1955), but the salinities ran higher than those given by Gunter (1945) for 1941 and lower than those of 1942. Probably this was due to the effects of local rains. The lowest salinities followed spring rains in April and May, 1949 and the highest came in August of the same year.

The Fishes

In all 10,633 fishes were caught in 144 hauls, an average of 73.8 fish per haul. There were 44 species, including six identified only as to genus. Twenty-four specimens, which were mostly small puffers, *Sphoeroides*, and scombroid fishes were listed as unidentified. All the fishes taken in this work were small species or the young of larger species. Almost all of them ranged from 20 to 99 mm. in total length, although the total range was 14 to

TABLE 1

The Water and Air Temperatures in Degrees Centrigrade Are Given for Each Station. The Air Temperatures Are in Parentheses.

Station	1	2	3	4	5	6	7	8
1947								
Nov. 9	20.5(22.7)	21.2(22.8)	———	———	———	———	———	———
Nov. 29	20.5(21.5)	19.0(.....)	18.8(...)	19.0(.....)	18.0(.....)	18.0(.....)	18.0(.....)	16.5(...)
Dec. 6	22.3(23.5)	23.0(20.6)	20.8(22.0)	20.5(22.6)	20.4(21.8)	20.8(21.8)	21.4(21.1)	23.2(21.6)
Dec. 31	22.3(21.1)	19.5(19.5)	19.5(19.8)	19.5(20.0)	19.3(20.2)	19.0(20.1)	19.0(20.0)	19.0(21.0)
1948								
Sept. 19	28.0(28.8)	28.5(29.5)	28.3(29.5)	28.0(27.8)	28.8(27.0)	28.5(28.0)	29.1(28.1)	29.5(28.0)
Sept. 26	22.7(22.7)	22.5(21.5)	24.2(22.2)	25.2(23.0)	25.3(23.2)	25.5(23.0)	26.2(23.0)	22.0(23.2)
Oct. 10	26.3(27.5)	26.5(28.0)	26.5(28.8)	26.8(28.0)	26.8(28.0)	27.0(27.5)	27.0(27.5)	28.5(27.8)
Oct. 31	24.2(25.4)	24.8(24.5)	24.6(25.5)	25.0(25.5)	24.7(26.2)	25.1(25.6)	25.5(25.5)	28.0(28.5)
Nov. 7	19.8(24.0)	23.0(24.0)	22.2(22.8)	21.5(22.0)	22.0(22.1)	23.5(22.0)	23.0(22.5)	———
Dec. 12	22.0(22.0)	19.0(21.3)	19.2(21.3)	18.8(20.5)	19.0(20.5)	19.0(21.8)	19.0(21.2)	20.0(20.0)
1949								
Apr. 10	23.8(25.2)	22.2(24.2)	23.2(26.0)	22.8(26.1)	23.0(26.4)	23.0(26.3)	22.3(26.0)	25.8(21.0)
Apr. 24	28.1(26.2)	23.7(25.1)	22.4(26.6)	24.8(24.0)	23.9(26.0)	24.2(25.0)	23.8(24.2)	26.0(24.6)
May 8	26.4(23.8)	21.8(28.8)	27.0(26.8)	27.1(26.8)	26.0(26.8)	27.0(27.0)	27.2(27.8)	30.5(28.8)
May 22	27.0(28.4)	26.8(27.5)	26.8(27.7)	27.4(28.2)	27.8(27.5)	28.0(28.5)	28.0(28.0)	29.8(30.0)
June 11	———	28.9(28.2)	29.0(28.8)	29.0(28.2)	29.0(28.1)	29.0(28.5)	29.0(28.5)	———
June 24	———	29.5(30.0)	30.0(29.8)	29.9(30.0)	30.0(29.8)	30.2(29.4)	30.1(29.8)	31.5(32.0)
July 9	———	29.0(30.0)	29.1(30.1)	29.3(30.1)	29.3(30.0)	30.0(30.0)	30.1(30.0)	31.5(30.5)
Aug. 7	———	27.5(29.0)	27.8(28.5)	28.0(28.5)	28.0(29.0)	28.0(29.0)	28.8(28.8)	29.8(31.0)
Aug. 20	———	31.4(29.9)	32.0(29.0)	32.0(28.9)	32.0(28.8)	32.0(29.1)	32.1(29.1)	———

TABLE 2

The Salinity in Parts Per Thousand Are Given for Each Station. The Determinations Were Made by Titration.

Station	1	2	3	4	5	6	7	8
1947								
Nov. 9	32.5	32.5	32.5	32.5	31.9	31.9	31.6	31.5
Nov. 29	29.2	29.1	29.4	29.2	29.3	29.0	29.2	25.8
Dec. 6	27.7	28.3	28.3	28.3	28.4	28.0	27.8	24.4
Dec. 31	31.5	31.7	31.7	31.6	31.8	31.8	31.8	31.8
1948								
Sept. 19	29.6	29.8	29.3	29.3	29.2	29.2	28.7	28.7
Sept. 26	28.5	28.4	28.0	28.0	28.0	27.9	27.9	28.1
Oct. 10	31.9	31.5	31.6	31.9	31.8	31.5	31.5	30.9
Oct. 31	31.5	31.1	31.2	31.0	31.0	31.0	30.9	31.0
Nov. 7	38.6	32.3	32.3	32.3	32.1	32.0	31.7	... .
Dec. 12	31.9	31.6	31.7	31.7	31.4	31.6	31.9	32.2
1949								
Apr. 10	29.3	32.3	32.3	32.2	31.9	32.2	31.4	29.8
Apr. 24	27.7	28.1	28.3	28.2	28.0	27.6	26.5	24.7
May 8	33.2	23.1	23.1	22.5	22.3	21.7	21.6	21.9
May 22	35.9	27.6	27.8	.... .	..	.. ...	.....	.... .
May 29	.....	.. .	.	32.9	32.7	32.9	32.3	31.9
June 11	.....	33.2	32.8	32.2	31.9	31.6	31.6	.. .
June 24	.....	34.7	34.6	34.3	34.1	34.00	33.9	33.6
July 9	.....	35.2	34.9	35.3	35.3	35.1	34.3	34.9
Aug. 17	.....	31.7	31.6	31.5	31.6	31.7	31.5	31.2
Aug. 20	.....	35.9	35.6	35.7	35.7	35.6	35.7	.... .

177 mm. Only eleven fish were as long or longer than 100 mm. These were: *Elops saurus*, *Strongylura timucu*, *Oligoplites saurus*, *Polydactylus octonemus*, *Mugil cephalus* 2, *M. curema* 2, *Trachinotus carolinus* 2, and *Menidia beryllina*. The last specimen was 114 mm. long, which is huge for that species.

The species and the numbers caught are listed in decreasing order in Table 3. It is divided into the three periods of the work, as shown in Tables 1 and 2. The pass and

TABLE 3

The Catch by Species at the Pass Stations and the Beach Stations Are Shown Separately for Each of the Three Periods of Work, With Totals and Average Catches.

	Nov.-Dec., 1947		Sept.-Dec., 1948		April-Aug., 1949		TOTALS		Beach
	Beach	Pass	Beach	Pass	Beach	Pass	Beach	Pass	and Pass
Trachinotus carolinus	73	1	170	.....	2,959	11	3,202	12	3,214
Harengula pensacolae	0	0	1,481	313	679	362	2,160	675	2,835
Mugil curema ..	4	15	3	64	468	590	475	669	1,144
Menidia beryllina	5	146	80	276	58	244	143	666	809
Fundulus similis	2	56	8	222	2	153	12	431	443
Anchoa mitchilli	3	4	208	5	171	0	382	9	391
Micropogon undulatus	0	0	0	2	238	0	238	2	240
Brevoortia sp.	0	0	0	0	190	0	190	0	190
Menticirrhus littoralis	23	0	47	0	119	0	189	0	189
Anchoa hepsetus	0	0	125	5	58	0	183	5	188
Cynoscion nothus	0	0	0	0	159	0	159	0	159
Cyprinodon variegatus	0	1	0	110	1	45	1	156	157
Caranx latus	0	0	0	0	117	4	117	4	121
Eucinostomus sp.	0	0	0	0	0	104	0	104	104
Stephanolepis hispidus	0	0	0	0	97	0	97	0	97
Polydactylus octonemus	0	0	0	0	95	0	95	0	95
Sciaenops ocellata	0	0	0	0	29	16	29	16	45
Syngnathus sp.	0	0	5	0	31	1	36	1	37
Anchoa sp.	0	0	2	0	30	0	32	0	32
Gobionellus boleosoma	0	0	0	0	0	27	0	27	27
Menticirrhus americanus	1	0	13	1	0	0	14	1	15
Trachinotus glaucus	0	0	0	0	14	0	14	0	14
Strongylura sp.	0	0	3	5	2	1	5	6	11
Others	6	7	19	13	29	2	54	23	76
Totals	117	230	2,164	1,016	5,546	1,560	7,827	2,806	10,633
Number of Hauls	24	8	36	11	55	10	115	29	144
Average per Haul	4.9	28.8	60.1	92.4	100.8	156.0	68.1	96.8	73.8

outside beach stations are also separated. At the two pass stations 2,806 fishes were caught. These are listed separately because certain fishes which are found in inside waters are not found in the outside beach waters. All of the gobies, *Gobionellus boleosoma,* and all *Cyprinodon variegatus* but one, were taken in the passes. Similarly, almost all *Fundulus similis* were taken inside. It was noted before (Gunter, 1945) that this species is not found on the outside beach, except for rare strays next to the mouths of the passes. The great majority of the silversides, *Menidia beryllina,* were taken in the pass. Gunter (op. cit., Table 24) has shown that this species and the Cyprinodontes are primarily bay fishes and that their restriction to such waters is not caused by salinity limits.

Eleven species, caught mostly on the beach, made up 0.1 per cent of the catch. Five species, *Trachinotus carolinus, Harengula pensacolae, Mugil curema., Anchoa mitchilli* and *Micropogon undulatus,* made up 82.4 per cent of the beach catch. The last three are scattered widely in the bays, too, but the first two are more abundant on the outer beach. The little pompano feed to a large extent on young *Harengula,* and are commonly found in the summer with their stomachs distended with them.

The average catch was consistently greater within the passes than on the beach. It appears that small fishes are more abundant in protected waters than on the open shore.

The 1947 catches may be called late fall catches. An average of 10.9 specimens were caught per haul. The average beach haul was quite low, 4.9 fish per haul. In six hauls nothing was caught and several hauls yielded only one fish. On the beach the most abundant fishes were the pompano, *Trachinotus carolinus,* and the Gulf whiting, *Menti-*

cirrhus littoralis. Menidia beryllina and *Fundulus similis* were the most abundant species in the passes.

The 1948 catches may be taken as late summer and fall catches. Forty-seven drags yielded 67.6 fish per haul. The silver sardine, *Harengula pensacolae*, the two anchovies, *Anchoa mitchilli* and *A. hepsetus*, and the pompano, *T. carolinus*, were the most abundant fishes on the beach, while *Harengula pensacolae, Menidia beryllina, Fundulus similis* and *Cyprinodon variegatus* were the most numerous in the passes.

The 1949 catches may be seasonally classified as spring and summer catches. An average of 109.3 fish per haul were caught from 65 hauls. On the beach the pompano, *T. carolinus*, the white mullet, *Mugil curema*, and the sardine, *Harengula pensacolae*, were dominant. *Mugil curema, Harengula pensacolae, Menidia beryllina*, and *Fundulus similis* were most abundant at the pass stations.

Ninety-six specimens of *Stephanolepis hispidus*, the filefish, were taken on the Gulf beach from April to August, 1949. They have not been reported there before. They ranged from 31 to 44 mm. long and were caught where the water salinities ranged from 21.7 to 34.8 *per mille*.

In addition to the more abundant fishes listed in Table 3 the following species were taken occasionally: *Strongylura sp., Eucinostomus sp., Mugil cephalus, Astroscopus y-graecum, Oligoplites saurus, Eucinostomus gula, Trachinotus falcatus, Eucinostomus argenteus, Membras sp., Chloroscombrus chrysurus, Strongylura timucu, Strongylura notata, Lobotes surinamensis, Anchoa lyolepis, Hyporhamphus unifasciatus, Elops saurus, Lagodon rhomboides, Pomatomus saltatrix, Abudefduf saxatilis, Selene vomer, Caranx sp., Alutera scripta, Sphoeroides sp.*

Characteristics of the Dominant Species Populations

The two chief beach fishes are the common pompano, *Trachinotus carolinus*, and the sardine, *Harengula pensacolae*. Both have offshore populations of larger individuals, but the young are restricted to the Gulf beach. The sardine is a plankton feeder and the young pompano seem to subsist largely upon them during their early life in the surf. These two fishes made up 69.3 per cent of the total beach catch. The mullet, *Mugil curema*, the anchovies, *Anchoa mitchilli* and *A. hepsetus*, and the small croaker, *Micropogon undulatus*, were common at times. These findings correspond to the work previously reported (Gunter, 1945) except that *Polydactylus octonemus* was found to be more abundant than *M. undulatus*.

At least three species of small pompano and possibly four were taken on the Mustang Island beach. One of these, which was called *Trachinotus argenteus* in the original notes, is here synonymized with *T. carolinus*, following Ginsburg (1952). It was separated at sizes up to 82 mm. but specimens are no longer available and the case is uncertain. Another species, at a size of 23 mm., was dusky or blackish, had reddish orange dorsal spines and a reddish orange eye. It seemed to be *T. falcatus*. It was taken in June, 1949. A third species, at a size of 23 mm., was reddish orange on the lower caudal lobe, the anal fin edge and large spine. It was called *T. goodei*, which Ginsburg synonymizes with *T. glaucus*, and probably belonged to the latter species.

Table 4 shows the size limits and crude modes of the pompano caught. It confirms the previous statement (Gunter, 1945) that the very young are recruited into the population over an extended period during the warmer months, indicating a long spawning season for the pompano on the Gulf coast.

TABLE 4

Length-frequency Data on the Pompano, *Trachinotus carolinus* Caught on the Gulf Beach of Mustang Island.

Years	Months	Size Limits mm.	Crude Mode	Number of Specimens
1947	November	20–123	Indeterminable	38
	December	83–142	Indeterminable	2
1948	September	21– 79	33	26
	October	19– 84	30	43
	November	27– 74	33	39
1949	April	14– 52	17	68
	May	15– 83	23	856
	June	13– 83	50	242
	July	16– 81	18	104
	August	14– 99	23	202

TABLE 5

Length-frequency Data on the Sardine, *Harengula pensacolae*, Caught on the Gulf Beach.

Years	Months	Size Limits mm.	Crude Mode	Number of Specimens
1948	September	23– 81	38 and 63	864
	October	29– 67	43 and 53	258
	November	28– 39	....	2
1949	April	25– 32	28	41
	May	27	....	1
	June	23– 52	28	366
	July	25– 67	28	30
	August	29– 93	47	141

Table 5 gives size limits and crude modes for the silver sardine, *Harengula pensacolae*. The data indicate a relatively long spawning season. Gunter (1945) has previously noted evidences of two spawning peaks during the summer and a low point of abundance in July. The same thing is indicated but not proven by these data. Similarly the peak of abundance was found to be in the fall.

SEASONAL AND LATITUDINAL COMPARISONS

There is a seasonal succession on the Gulf beach, which can be partially characterized as the result of this and the previous work (Gunter, 1945). In most years the beach is practically unpopulated in winter except for a few bay fishes next to the passes. In some years this depopulation shows up in December, but in others it comes as early as October. Besides the diminution in numbers or absence of many species in the cooler months there is a slow change in the complex of a few dominant species, which is doubtless different each year. Table 6, lists the species in order of their abundance for the seasons. The complexes for the different years are different, but the pompano and sardine are generally present in considerable numbers except during the cooler months.

Such seasonal successions are quite different from those on a plot of grassland or marine fouling organisms on an underwater object. In the latter, what happens or what is present at a given season depends somewhat on what was present before. In fish populations, which grow as individuals and migrate about, the connections with their successors are much more tenuous and there is no proof that the midwinter population would not be the same if the summer population had been altogether different.

Pearse, Humm and Wharton (1942) found that the silverside, *Menidia menidia*, the anchovy, *Anchoa mitchilli*, and the pompano, *Trachinotus carolinus*, were the most

TABLE 6

A Comparison of the Most Abundant Species on the Gulf Beach as Found by Gunter (1945) in 1941–42 and the Present Work 1947–49, at the Different Seasons. The Fishes are Listed in Order of their Abundance.

	Gunter (1945)	Present data	Number
Spring	*Anchoa mitchilli*	*Trachinotus carolinus*	1,076
	Mugil cephalus	*Mugil curema*	420
	Polydactylus octonemus	*Micropogon undulatus*	232
Summer	*Polydactylus octonemus*	*Trachinotus carolinus*	905
	Harengula pensacolae	*Harengula pensacolae*	605
	Trachinotus carolinus	*Brevoortia sp.*	155
Fall	*Anchoa mitchilli*	*Harengula pensacolae*	1,481
	Harengula pensacolae	*Trachinotus carolinus*	246
	Trachinotus carolinus	*Anchoa hepsetus*	132
Winter	*Mugil cephalus*	*Menidia beryllina*	61
	Anchoa mitchilli	*Fundulus similis*	10

abundant fishes on an outside beach at Beaufort, North Carolina, during the summer of 1939. The next summer the most abundant species were *M. menidia, Fundulus majalis,* and *T. carolinus.* The two stations where these hauls were made are close to the broad inlet into Beaufort Harbor, which may account for the presence of *M. menidia* and *F. majalis.* Nevertheless, the association seems to be much the same. The species are the same or are cognates of those commonly found on the Texas coast.

Warfel and Merriman (1944) worked an inside New England beach. Among the six most abundant fishes were *Menidia menidia, Fundulus majalis* and *Brevoortia tyrannus.* The New England populations of beach fishes are more similar to those of North Carolina than to those of Texas, but several of the abundant species are cognates of those common on Texas shores. It appears that over such great distances as from South Texas to southern New England the populations of small beach fishes are similar.

Summary

1. A study of fish populations was made in Aransas and Corpus Christi passes and the outer beach of Mustang Island in South Texas. Eight stations were sampled by small-mesh seine hauls eighteen times in three different years, 144 hauls being made. Water temperatures and salinities were taken at each station.

2. The fishes taken were all small and only 11 were greater than 100 mm. in length. The total catch, representing 44 species, was 10,633 fishes. The most abundant species were: *Trachinotus carolinus, Harengula pensacolae, Mugil curema, Menidia beryllina, Fundulus similis* and *Anchoa mitchilli.* Five species, *T. carolinus, H. pensacolae, M. curema, A. mitchilli* and *Micropogon undulatus,* made up 82.5 per cent of the beach catch. The last three are common bay fishes, but the first two are abundant only on the beach and in outside waters.

3. Fishes were most abundant on the beach in the spring and summer, less abundant in late summer and fall, and quite scarce in late fall and early winter. The Gulf beach is primarily a habitat of young pompano, *T. carolinus,* and the sardine, *H. pensacolae;* these two fishes made up 69.3 per cent of the catch. Comparisons made with seine hauls of earlier years showed some change of the populations based upon fluctuations of a few species.

4. The dominant species of the beach were the same species or species cognate to

those of North Carolina beaches, and they were all cognates of those reported from New England beaches.

5. All *Gobionellus boleosoma*, nearly all *Cyprinodon variegatus* and *Fundulus similis*, and the great majority of *Menidia beryllina*, were taken in the passes rather than on the outside beach. More fishes were caught per haul at the stations inside the passes than on the open beach, but the species were somewhat different. Four species, *H. pensacolae*, *Mugil curema*, *M. beryllina*, and *F. similis* made up 87.0 per cent of the pass catch.

6. The work confirms previous findings that young pompano are recruited into the population over an extended period during warm months. It also supports reports of a double spawning peak for *H. pensacolae*. Small specimens of the filefish, *Stephanolepis hispidus*, are reported from the beach for the first time.

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Ecology and Taxonomy of Recent Marine Ostracodes in the Bimini Area, Great Bahama Bank

LOUIS S. KORNICKER

Institute of Marine Science, The University of Texas, Port Aransas, Texas

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Abstract

Areal distributions of kinds and abundance of both living and dead ostracodes in the Bimini area have been mapped on a photogrammetric base. Evidence was found indicating that substrate, salinity and current velocity affected distribution of ostracodes. Dissolved oxygen, pH, water color, organic detritus, organic content of the sediment, water depth, and daily temperature variation had little effect. Ostracodes, belonging to the suborder Myodocopa, were abundant in the Bimini area, but their shells decomposed after death and were absent from the sediment. The sediments containing the largest number of dead ostracodes did not occur in areas containing the largest number of living ostracodes. In North Sound and Cavelle Pond living ostracode species differed in kind from dead ostracodes contained in the sediment.

Introduction

Ostracodes have been extremely useful to geologists as stratigraphic markers. Their small size and abundance in many formations make it possible to study a whole fauna even though the available sample may be very small. The ostracode has the longest

range of any group used extensively for stratigraphic correlations. Many recent species seem to extend backward into the Tertiary unchanged.

Principally because of the importance of ostracodes to geology, fossil ostracodes are better known than those living in today's seas. The present study was undertaken in order to determine some of the environmental factors possibly influencing the distribution of living marine ostracodes. Information of this sort is useful in interpreting conditions which were in existence during the formation of fossil ostracode-bearing strata.

Another phase of the present study was the comparison of the areal distribution, abundance and kinds of living ostracodes with ostracode shells contained in the sediment. Ostracode shells in recent sediment are potential fossils. Knowledge of the relationship between the living animals and their remains is useful for understanding the limitations of fossil material used to infer ancient environments and faunas.

This study was made in the vicinity of the Bimini Islands, which are situated in the northwestern part of the Great Bahama Bank (Fig. 1). The sample area covers approximately 320 square kilometers in the shallow waters east of the Bank rim. An ecological study in the Bahamian region becomes especially significant because the warm, clear shelf sea of this area probably typifies limestone-forming seas which covered a large part of the continents in the past.

Among the environmental factors considered in this study are salinity, temperature, dissolved oxygen, pH, water depth and color, current velocities and direction, type of sediment and its organic content, presence or absence of organic detritus, and the biota.

The Ostracoda are usually divided into four suborders: 1) Myodocopa, 2) Podocopa, 3) Cladocopa, 4) Platycopa. Only members of the suborders Podocopa and Platycopa occur in abundance as fossils, although the Myodocopa extend backward into the Silurian and the Cladocopa at least into the Jurassic. This seems principally because many members of the suborders Podocopa and Platycopa bear shells strongly fortified with calcium carbonate, which makes them more easily preserved than members of the suborders Myodocopa and Cladocopa, which have shells with less calcium carbonate. The systematics of the Myodocopa encountered in the Bahama area are considered in this paper. Systematics of others suborders are to follow. The suborder Myodocopa is represented in Bimini waters by 10 genera, two of which are new, and 19 species, which include 14 new species and one new subspecies.

Acknowledgments

Data are from a Ph.D. dissertation, *Ecology and Taxonomy of Recent Marine Ostracodes in the Bimini Area, Great Bahama Bank*, 1957, Columbia University. The study was made as part of a biogeological survey of the northwestern part of the Great Bahama Bank under the direction of Professors N. D. Newell and John Imbrie and made possible through grants from the Humble Oil and Refining Company, Gulf Research and Development Company, the Shell Development Company, and Esso Research and Engineering Company. Free exchange of samples and data with Mr. Edward G. Purdy and Dr. Robert J. Menzies, who also were doing field work in the Bimini area, is gratefully acknowledged. Dr. R. S. Humm kindly identified algal specimens. The manuscript has been criticized by Mr. I. Gregory Sohn and Dr. Stuart A. Levinson. The base for the field operations was the Lerner Marine Laboratory of the American Museum of Natural History. The excellent facilities of this laboratory are greatly appreciated.

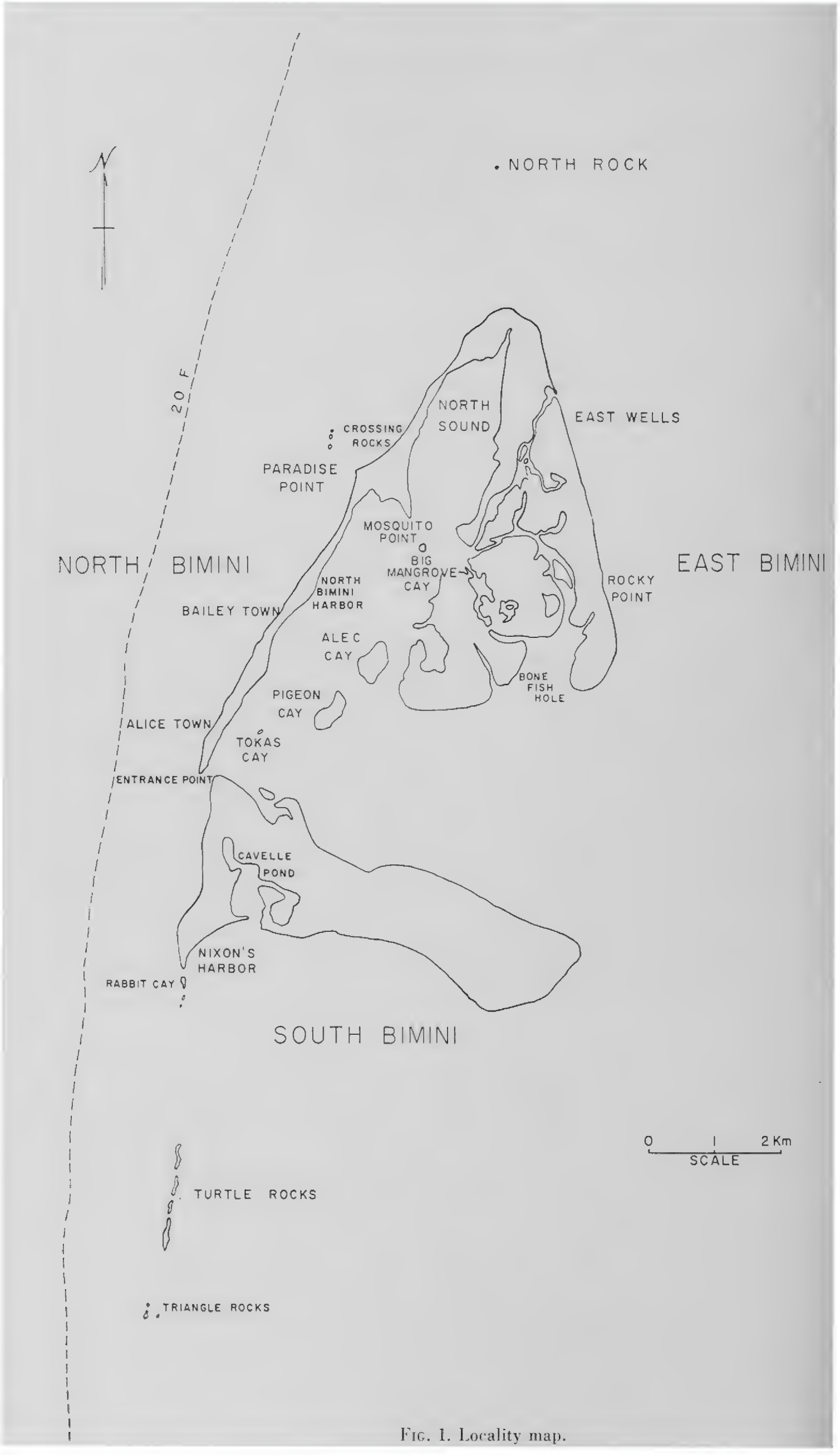

FIG. 1. Locality map.

Almost all of the underwater photographs and the photographs of ostracodes were taken by Mr. G. Robert Adlington of the American Museum. Final drawings were done, under the supervision of the writer, by Mr. and Mrs. T. O'Callaghan.

The map insert which gives the distribution of bottom types in the Bimini-Cat Cay area is the result of a joint effort by Professor Newell, Professor Imbrie, Mr. Purdy, Mr. William G. Heaslip, and the writer, and is published with the permission of the collaborators.

Methods

Precise geographic location of sample stations was made possible by using photogrammetric base maps showing submarine configurations. Clarity of Bahamian waters made this procedure practical. In addition, since much of the work was done within sight of land, it was usually possible to fix the station location from horizontal sextant angles which were plotted in the field using a three-arm protractor (Shepard, 1948).

Most of the samples used for quantitative estimates of the number of living and dead ostracodes in the sediment at the station locations were obtained using a modification of the Petersen grab designed by Dr. K. O. Emery (Fig. 2). Samples obtained by hand using self-contained underwater breathing apparatus and by shallow water diving were used principally for sediment analysis.

FIG. 2. Emery grab sampler.

Walton (1955) in mapping the distribution of benthonic Foraminifera in Todos Santos Bay, Baja California, cored the bottom and used the top centimeter of the core for a standard sample. This method is not feasible on rock bottoms covered by less than one centimeter of sand. In the Bimini area rock covers an extensive area of the bottom and for this reason bottom cores were not used in the present study. The Emery grab sampler was found to collect successfully from rock bottoms covered by both thick and thin sand layers; therefore, practically all samples used for obtaining estimates of ostracode abundance were obtained using the Emery sampler. A 10 cc. subsample was removed from the larger sample to serve as the standard sample used in obtaining estimates of living ostracode abundance.

There are difficulties in comparing samples from different bottom types. For example, 10 cc. of sand from a rock bottom covered by less than one centimeter of sand represents more surface area than 10 cc. of sand obtained from a grab sample which includes sand from several centimeters depth. However, the results of the investigation indicate that major variations in ostracode abundance have not been masked.

Although the living ostracode abundance is based on 10 cc. samples, 10 grams of this sample were used to arrive at estimates of dead ostracode abundance. This was done so that the results of this investigation could be used more readily in making future comparisons with ostracode abundance in ancient lithified sediment. As the sediment parameters were fairly uniform, the abundance distribution patterns would have been about the same if the dead ostracode abundance had been based on 10 cc. samples, but the absolute numbers in each sample would have been somewhat higher.

Living ostracodes were hand-picked from the 10 cc. sample under a binocular microscope while the ostracodes were still alive. In this way the ostracode movement aided in differentiating the ostracode from the sediment, and living ostracodes could be readily separated from dead ostracodes or molted shells which contained remnants of appendages. Empty carapaces were removed from the dried 10-gram sample by alcohol flotation (Kornicker, 1957b). The alcohol flotation method resulted in further sampling error, as only 40 to 50 percent of the articulated carapaces and practically none of the disarticulated carapaces were removed from the sample. However, as all samples were treated in the same manner, relative variation in geographic abundance should be about the same; but the absolute number per sample will be smaller. Scanning of the residue of a few samples indicated that the concentrate contained representatives of all common species present in the residue. To facilitate removal of ostracodes from the alcohol concentrate, it was split into two fractions by sieving through a 124 micron screen. The areal distribution of the ostracode content of each fraction was analyzed separately.

A triangular trawl covered with fine netting was dragged over the sediment and through grass and algae in order to secure larger samples of the ostracode community than could be obtained with the Emery grab. Surface plankton samples were obtained by towing a half-meter net for about 20 minutes.

At each sample locality specific information was recorded concerning the depth and temperature of the water, thickness of the sand, substrate, macrofauna and flora living in the immediate area, and presence or absence of organic detritus. Water samples were analyzed for salinity by the Mohr method using silver nitrate. Selected sediment samples were analyzed for organic carbon using Schollenberger's (1927) method as modified by Allison (1935). Dissolved oxygen was determined using the standard Winkler method. Water color was determined with a Taylor Color Comparator. Hydrogen-ion

concentration of selected samples was obtained using a colorometric type pH meter manufactured by W. A. Taylor and Company. The pH values were corrected for salt error from the table given by Harvey (1955, p. 157). Cresol Red, which covers the range of pH values 7.2–8.8, was used as an indicator. Current velocity measurements were made with an Atlas Flowmeter attached to the end of a long pole in order to obtain bottom velocities. Current directions were determined by charting the direction of movement of floats (weighted balloons) and dye markers released from an anchored boat.

General Patterns of Ostracode Distribution

The areal distributions of living ostracodes collected in 10 cc. standard samples (Figs. 3, 5) are interpreted in Figures 4 and 6. In making these interpretive distribution maps, ostracode abundance limits were chosen to bring out the effect of environmental factors

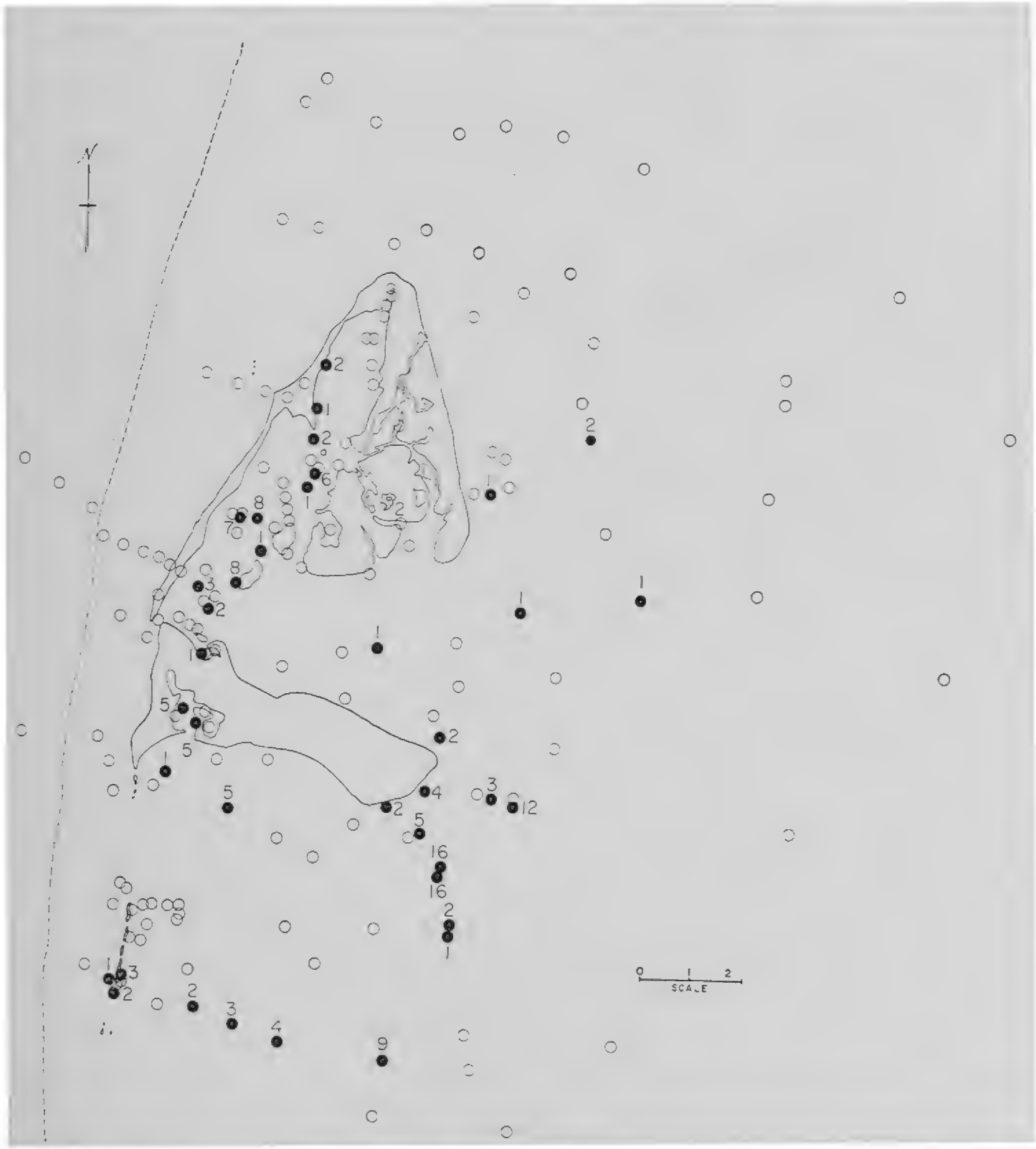

FIG. 3. Areal distribution of total living Myodocopa. Numerals indicate the number of specimens per sample (10 cc.). Clear circles indicate collections were made without finding individuals.

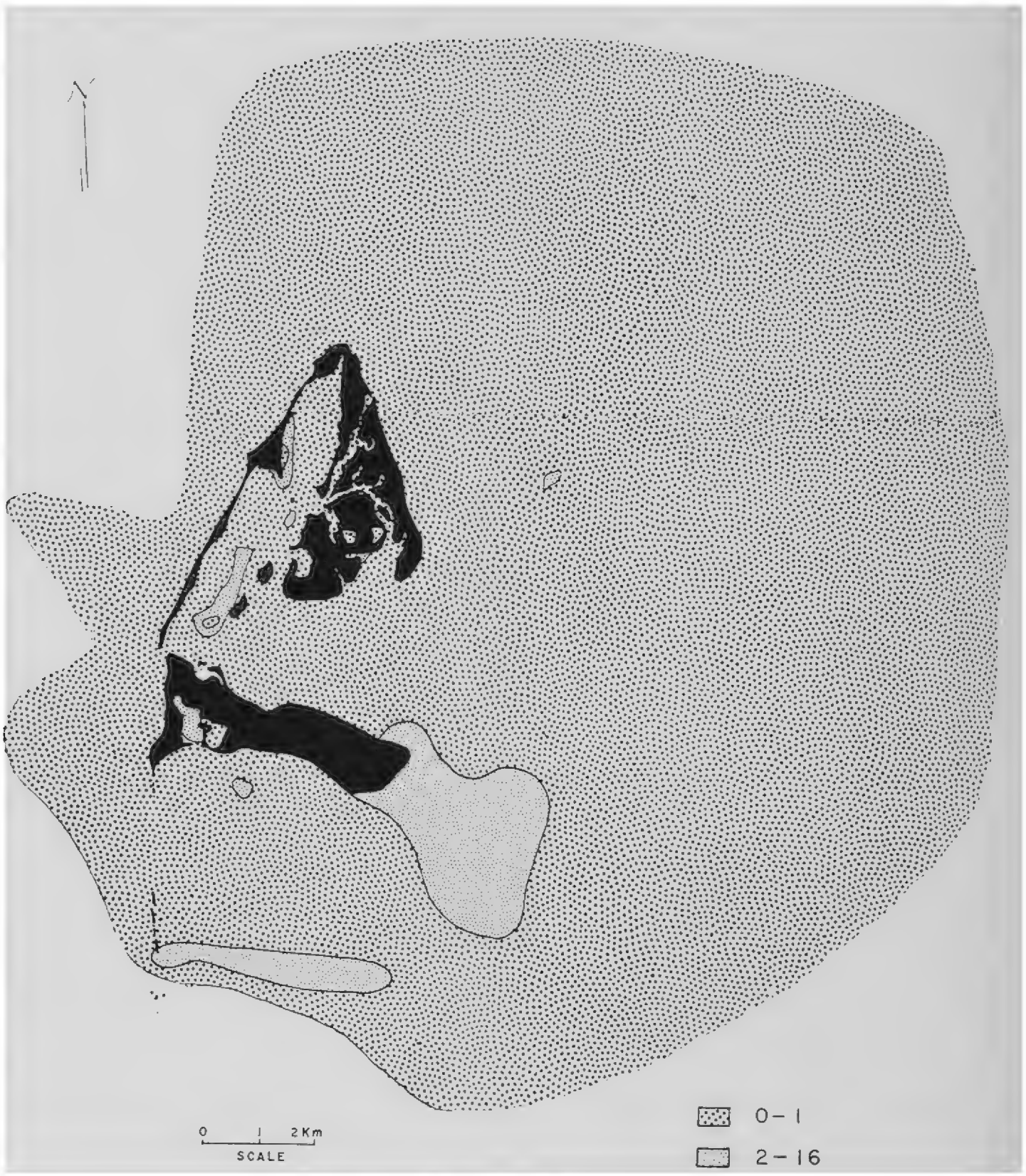

FIG. 4. Areal distribution of total living Myodocopa. The shading indicates the number of specimens per sample (10 cc.).

on ostracode abundance. For example, the effect of oolite bottom on Myodocopa distribution was best brought out by choosing limits of 0–1, 2–16 units, whereas limits of 0, 1–5, 6–40 were used for the combined Podocopa-Platycopa. Ostracode groups for interpretative maps representing the dead ostracode distribution were chosen on the same basis (Figs. 7–10). Causal environmental factors contributing to these areal distribution patterns are considered under later discussion of environment.

Only two out of 22 surface plankton tows taken in the vicinity of the Bimini Islands produced ostracodes. In one of these, obtained about 9 p.m., June 8, 1956, off the Lerner Marine Laboratory dock in North Bimini harbor, *Philomedes multichelata* Kornicker, a new species, was abundant and was evidently swarming. Several specimens were dissected and found to be males. No other ostracode species was in this haul. One

specimen of *Cypridina squamosa lerneri* Kornicker, a new subspecies, was collected from the same locality at 10 p.m., December 11, 1956. No halocyprids were captured in the Bimini vicinity either in the plankton tows or bottom samples.

Living ostracode collections were made in June and December, 1956. Identification of species in these samples was restricted primarily to the suborder Myodocopa. With the exception of *Asteropina extrachelata* Kornicker, a new species, of which only one individual was collected in June, 1956, all species were in the area during both collecting periods. Further work is needed to determine seasonal variations in ostracode abundance. The abundance and distribution of species belonging to the suborder Myodocopa are discussed along with species descriptions in the section on systematics.

FIG. 5. Areal distribution of living Podocopa and Platycopa. Numbers indicate the total number of specimens per sample (10 cc.).

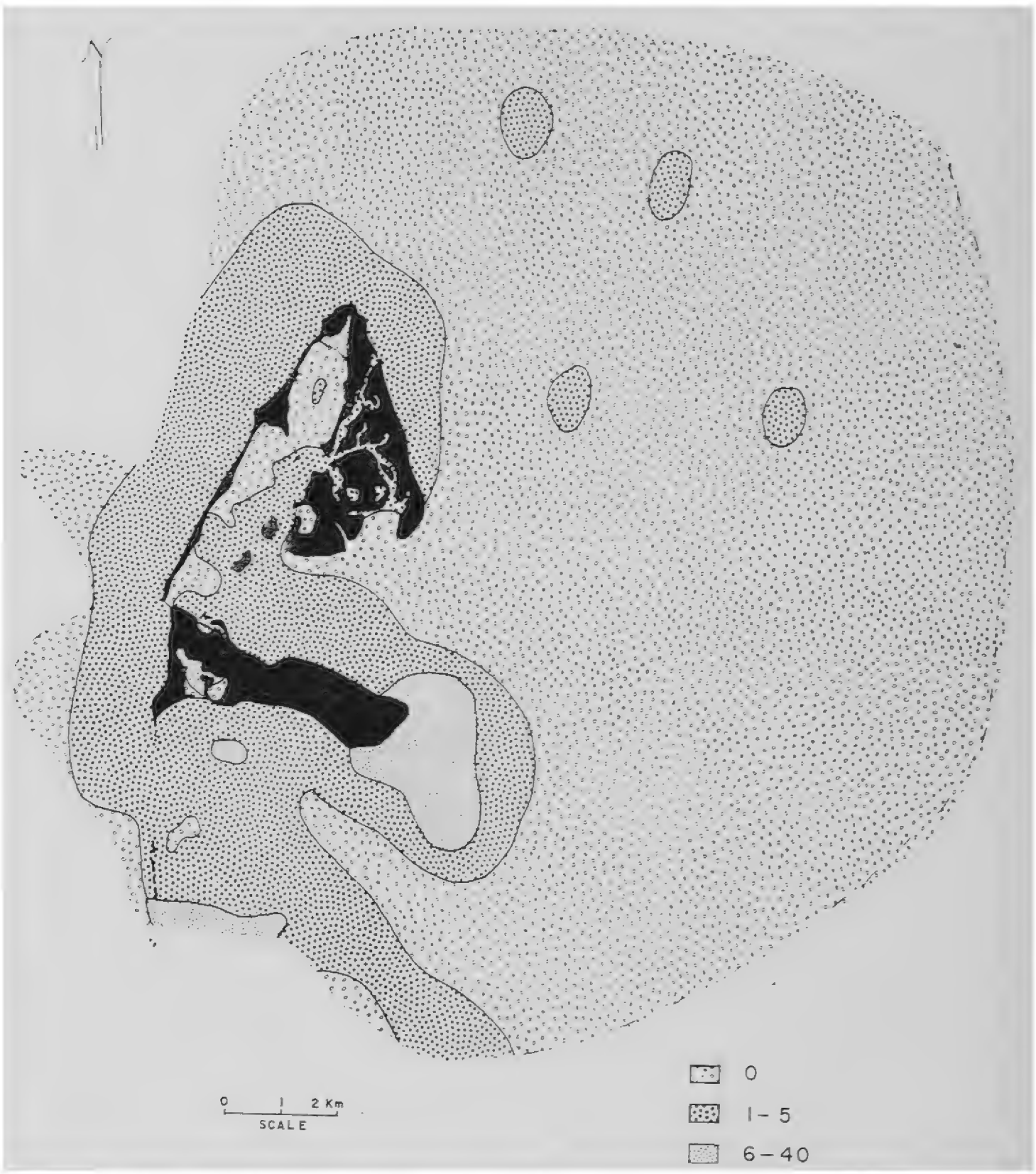

FIG. 6. Areal distribution of living Podocopa and Platycopa. Numbers indicate the total number of specimens per sample (10 cc.).

Environmental Factors Affecting Ostracode Distribution

INFLUENCE OF SUBSTRATE ON OSTRACODE DISTRIBUTION

The sediments in the Bimini area have been subdivided by Mr. Purdy and the writer into six facies:[1] chalky facies (I), pitted facies (II), unpitted facies (III), glazed facies (IV), faecal pellet facies (V), and oolite facies (VI). Figure 11 represents the areal distribution of these facies. These facies are distinguishable visually under a binocular microscope and have peculiar physical and chemical properties. Characteristic properties of the sediments of facies I, II, IV and VI are presented in Table 1.

[1] Facies is here used to define a geographical area covered by sediments distinguishable on the basis of physical, chemical, or biological properties from contemporary sediments covering adjacent or nearby areas.

TABLE 1.

	Chalky facies I	Pitted facies II	Glazed facies IV	Oolite facies VI
Dry Bulk Density, gm/cc*	1.0	1.45	1.45	1.6
Organic Carbon, % dry wt.	0.7	0.5	0.5	0.4
Median Diameter, mm.**	0.28	0.26	0.28	0.26
Sorting Index, (So)**	1.80	1.35	1.26	1.20

* Dry bulk density was obtained by weighing a known volume (10 cc) of dried sediment.
** Data supplied by Edward G. Purdy. For definition of So see Krumbein and Pettijohn (1938).

A description of each facies follows:

Chalky facies (I): The sediments within North Bimini harbor and North Sound, with the exception of the northern end of the latter region, consist of bioclastics which often appear chalky and are mixed with extremely fine-grained particles of calcium carbonate (mostly aragonite). These sediments do not pack well, and the dry bulk density is

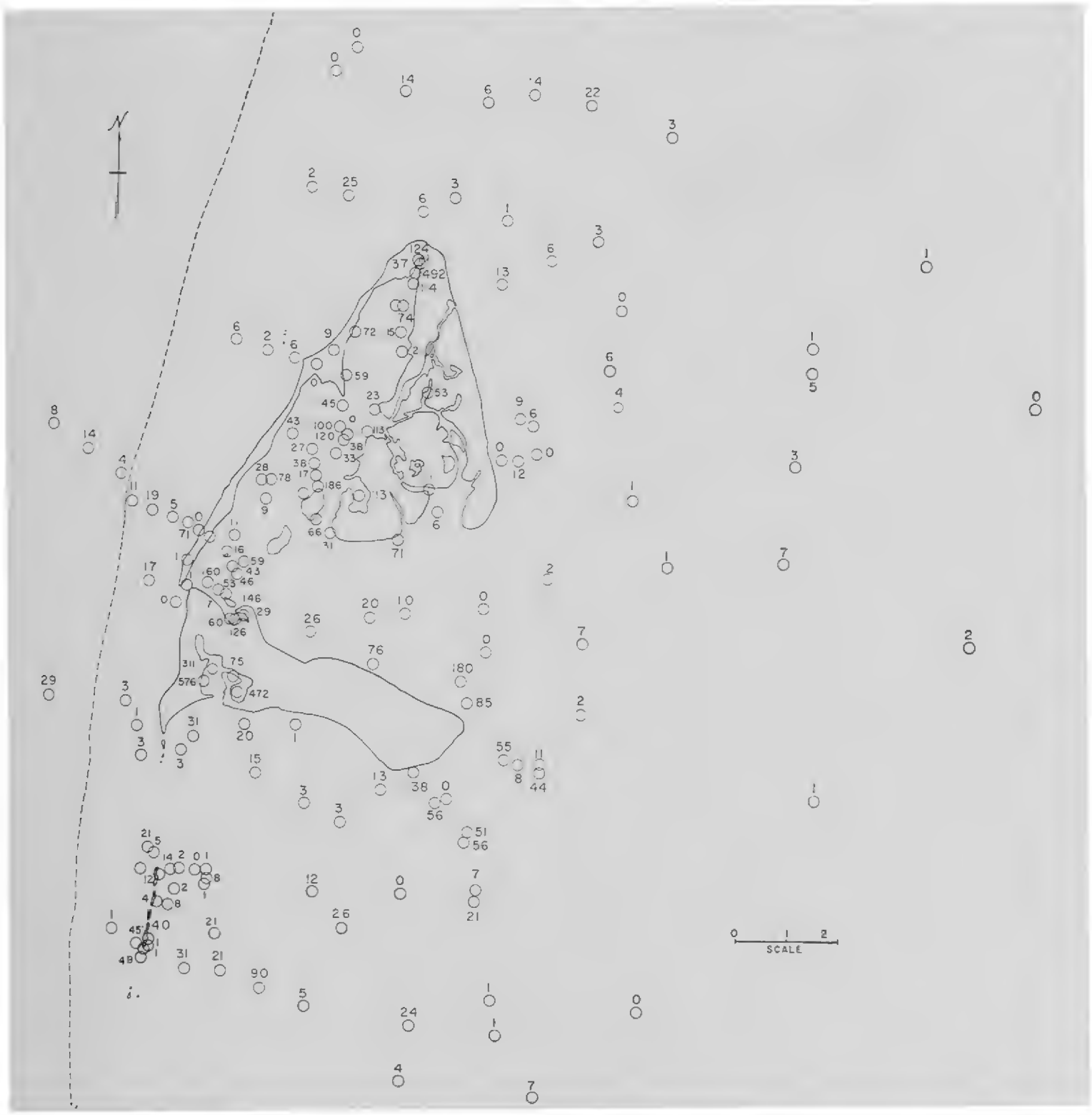

FIG. 7. Areal distribution of dead Podocopa and Platycopa. Numbers indicate the total number of specimens per 10-gram sample (larger than 124 M fraction).

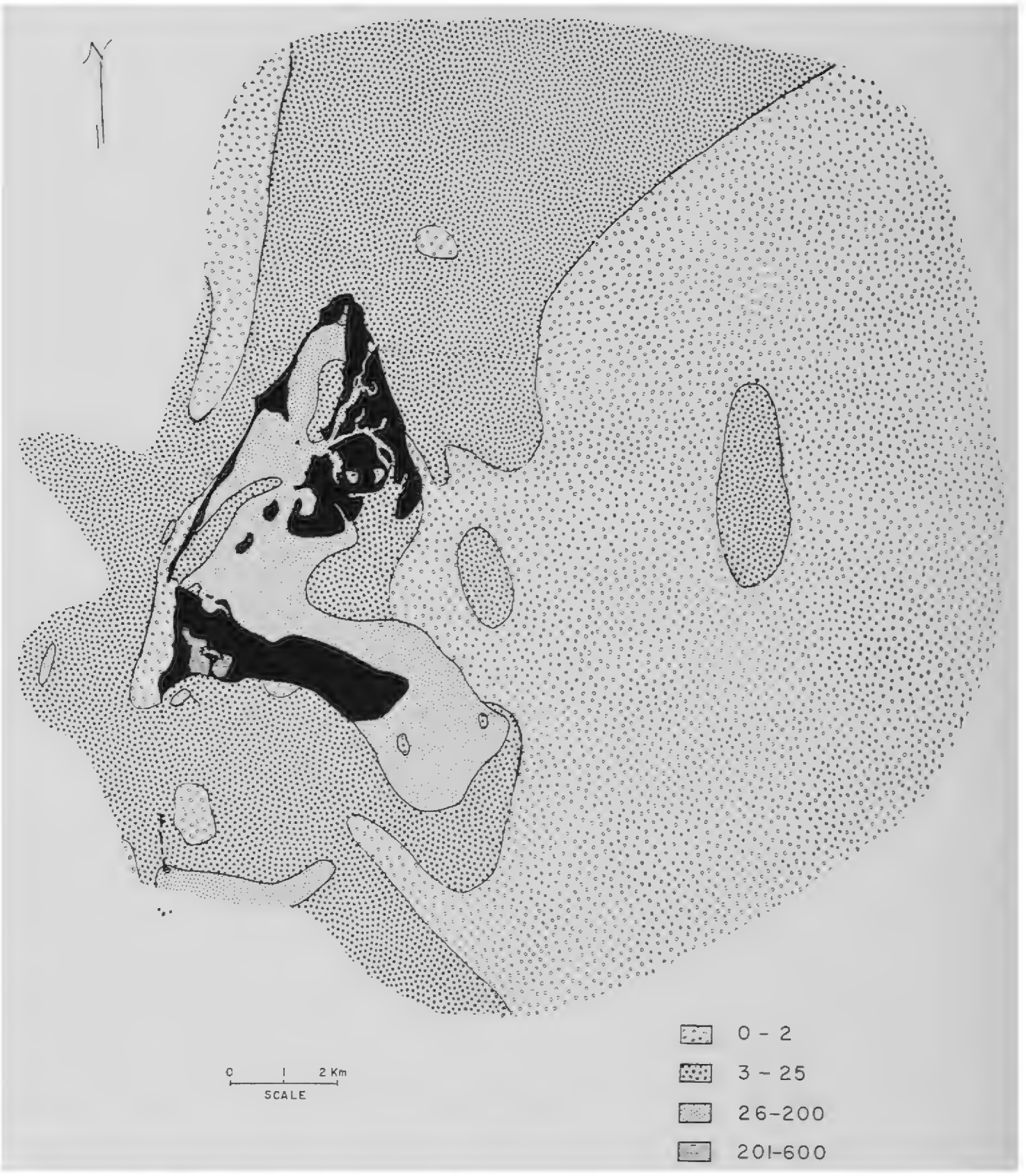

FIG. 8. Areal distribution of total dead Podocopa and Platycopa. Numbers indicate the total number of specimens per 10-gram sample (larger than 124 M fraction).

very low (about 1.0 gms./cc.). Because of the presence of the fine material, the sorting index (SO) is relatively high (about 1.8).

The region covered by this facies includes extensive areas partially exposed at low tide, tidal channels traversed by fairly rapid currents, thickly vegetated sand as well as sand virtually barren of plants, and rock bottom areas covered by a few millimeters of sand (Figs. 12–15). Organic detritus forms a film over the sediment in practically all of this region, and the organic carbon content of the sediment is higher than in the sediments on the Banks or outer platform.

The abundance of living ostracodes within the area covered by this facies varies. Myodocopa, Platycopa, and Podocopa are common over most of the region. The abun-

dance of dead shells of Podocopa and Platycopa is unusually high. This is thought to be the result of a high rate of ostracode accumulation in comparison to the rates of accumulation of preservable remains of other organisms.

Pitted facies (II) : Bioclastic sediments which have been subjected to intense pitting. possibly by algae, are situated south of South Bimini and extend into the deeper waters west of Turtle Rocks. These sediments form a thin layer from a few millimeters to a meter or so in thickness on top of the submarine platform from which the Bimini Islands

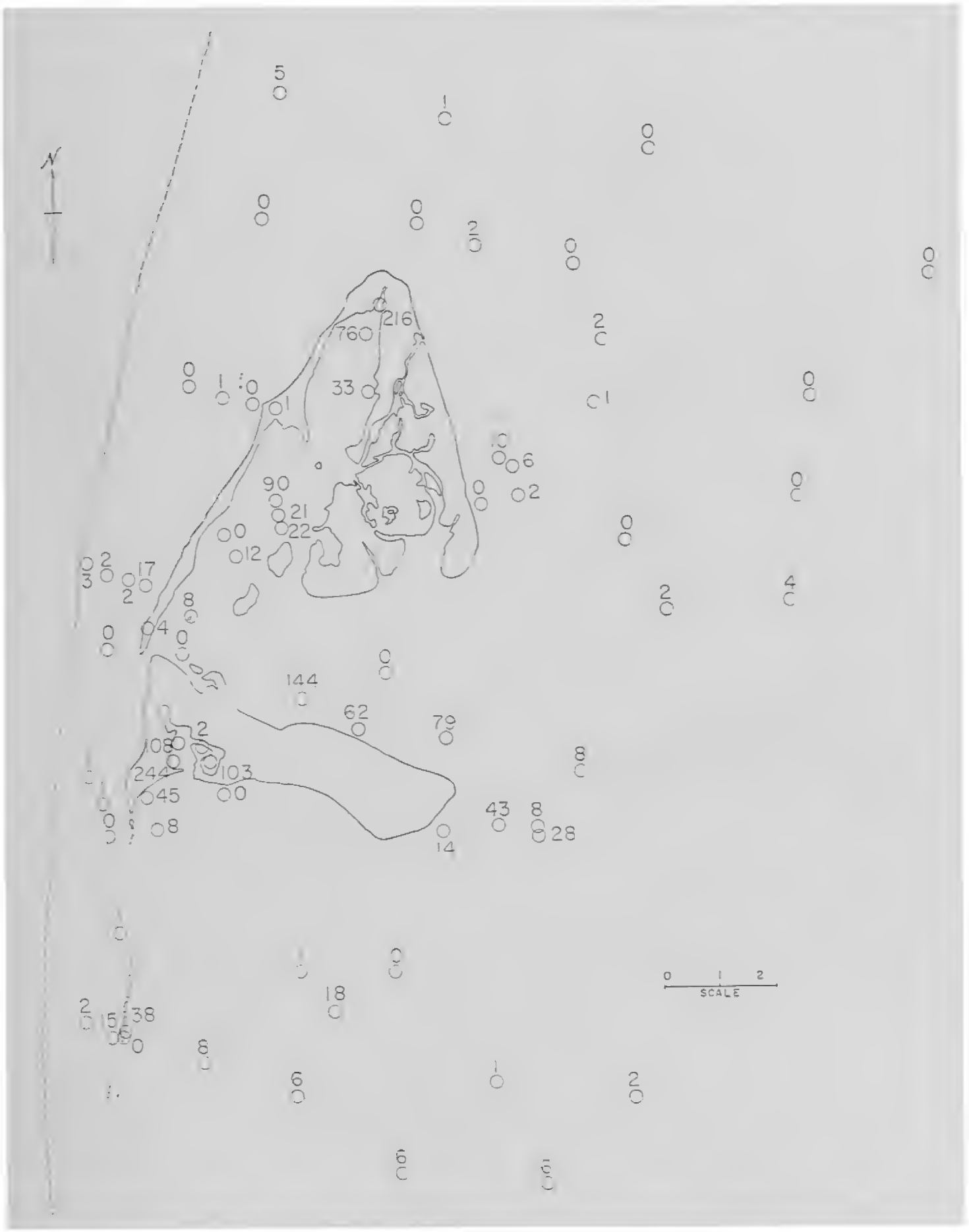

FIG. 9. Areal distribution of dead Podocopa and Platycopa. Numbers indicate the number of specimens per 10-gram sample (smaller than 124 M fraction).

and numerous cays project. The sediments of this facies butt against and blend with oolitic sediments which delimit this facies on the east.

Although sand, often supporting profuse vegetation, usually of *Thalassia*, is accumulating in the protected near-land areas, a large part of the region covered by pitted bioclastics is rock bottom containing small pockets of sediment or at most a film of sand a few millimeters thick. Where a rock bottom is present, a varied algal flora, often dominated by the genus *Sargassum*, combine with sea whips, corals, and sponges to form a community rich in numbers and diversity (Figs. 16–21).

FIG. 10. Areal distribution of total dead Podocopa and Platycopa. Numbers indicate the number of specimens per 10-gram sample (smaller than 124 M fraction).

Living ostraode abundance in the area covered by this facies is variable. Living ostracodes are common over most of the area but extremely abundant east of South Bimini and in a narrow strip just south of Turtle Rocks. The reason for this abundance is not known. The distribution of the dead ostracodes here is similar to that of the living ostracodes.

Unpitted facies (III): The sediments within Cavelle Pond are well preserved bioclastics and do not exhibit intensive pitting.

Cavelle Pond supports a profuse vegetation. The western segment of the Pond contains *Thalassia* as the dominant flora, whereas *Laurencia* is dominant in the eastern part. The passageway which connects the two segments is covered in many places by only 15 cm. of water at low tide.

Living ostracodes are common in this pond. In general, the same species living here are living in other marine environments in the Bimini vicinity. Dead ostracodes are extremely abundant and consist predominantly of brackish water forms not living in Cavelle Pond at present. These shells are probably relicts from the time Cavelle Pond

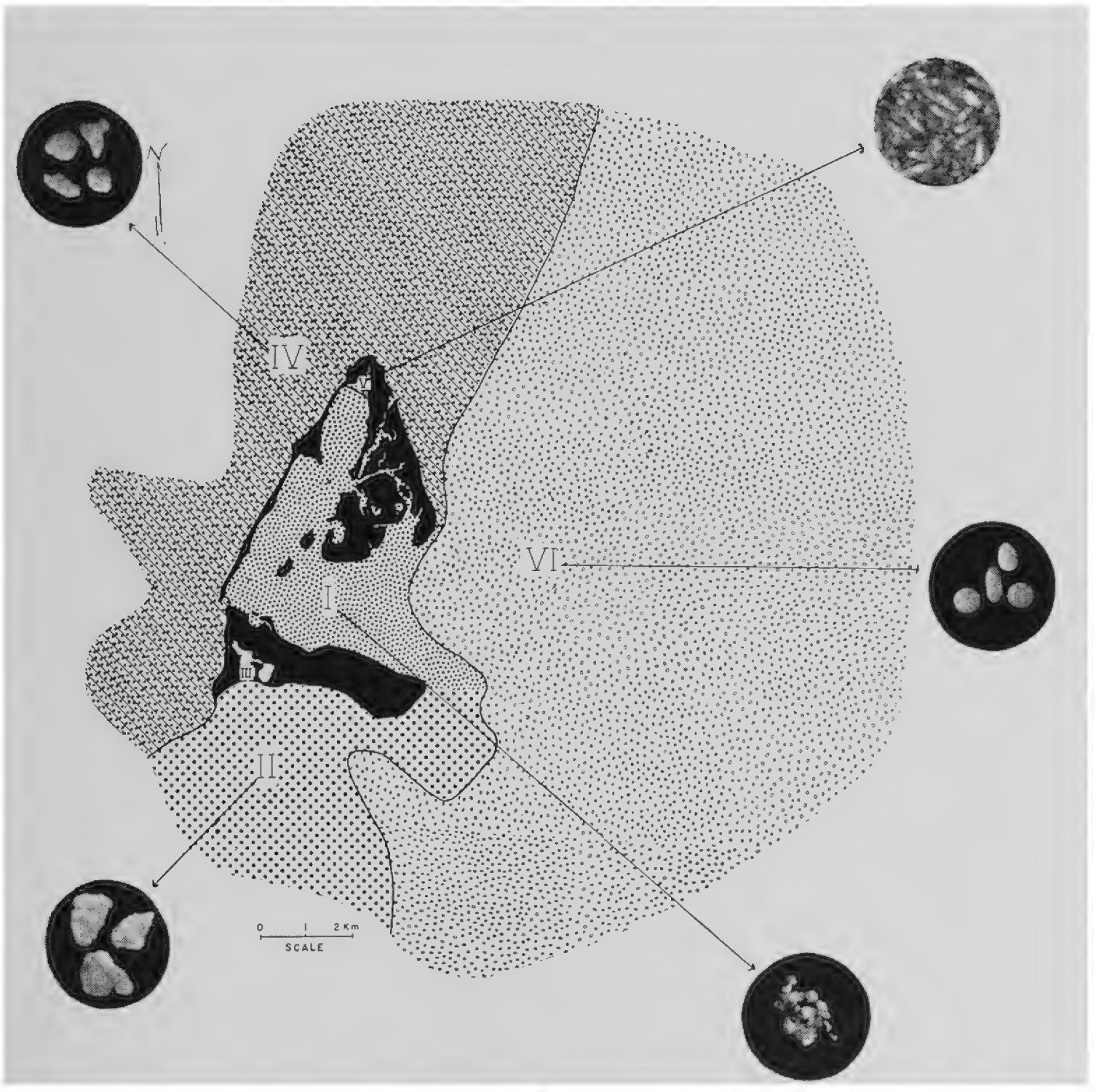

FIG. 11. Sediment facies map. I, chalky facies; II, pitted facies; III, unpitted facies; IV, glazed facies; V, faecal pellet facies; VI, oolite facies.

FIG. 12. Intertidal zone, North Bimini Harbor in front of Lerner Marine Laboratory. Mounds in foreground are formed by the worm *Arenicola*.

was separated from the sea and contained brackish water (see section on "Salinity").

Glazed facies (IV) : Bioclastics which are rounded and appear glazed form the beach sands and sediment along the western shores of North and South Bimini. Aggregates of the glazed grains are common where the glazed bioclastics blend with oolite sands around the northern end of North Bimini.

The shifting sands which are parallel to the coast line support little vegetation, although isolated patches of *Thalassia* and *Chondria tenuissima* (Goodenough and Woodward) appear to be thriving on this substrate. Rock-bottom areas off the coast are covered by only a film of sand. These support abundant and diverse plant and animal life (Figs. 22, 23).

Living and dead ostracodes are rare in the area covered by this facies. The rock-bottom areas seem to contain more ostracodes than the surrounding sand areas. The rarity of ostracodes in this region is considered to be the result of agitation of the sand by waves. Ostracodes are, for the most part, burrowing animals, and many species may not be adapted for existence in shifting sand.

Faecal pellet facies (V) : Faecal pellets of the gastropod *Batillaria minima* were abundant in the sediment in the extreme northern end of North Sound (Kornicker and

Purdy, 1957). Although the lime-secreting organisms (ostracodes, Foraminifera, pelecypods, gastropods) form but a small percentage of the total sediment in the upper few centimeters, their proportion materially increases in the sediment below the surface due to poor preservation of the faecal pellets.

Myodocopa are absent from the area covered by this facies. This is thought to be the

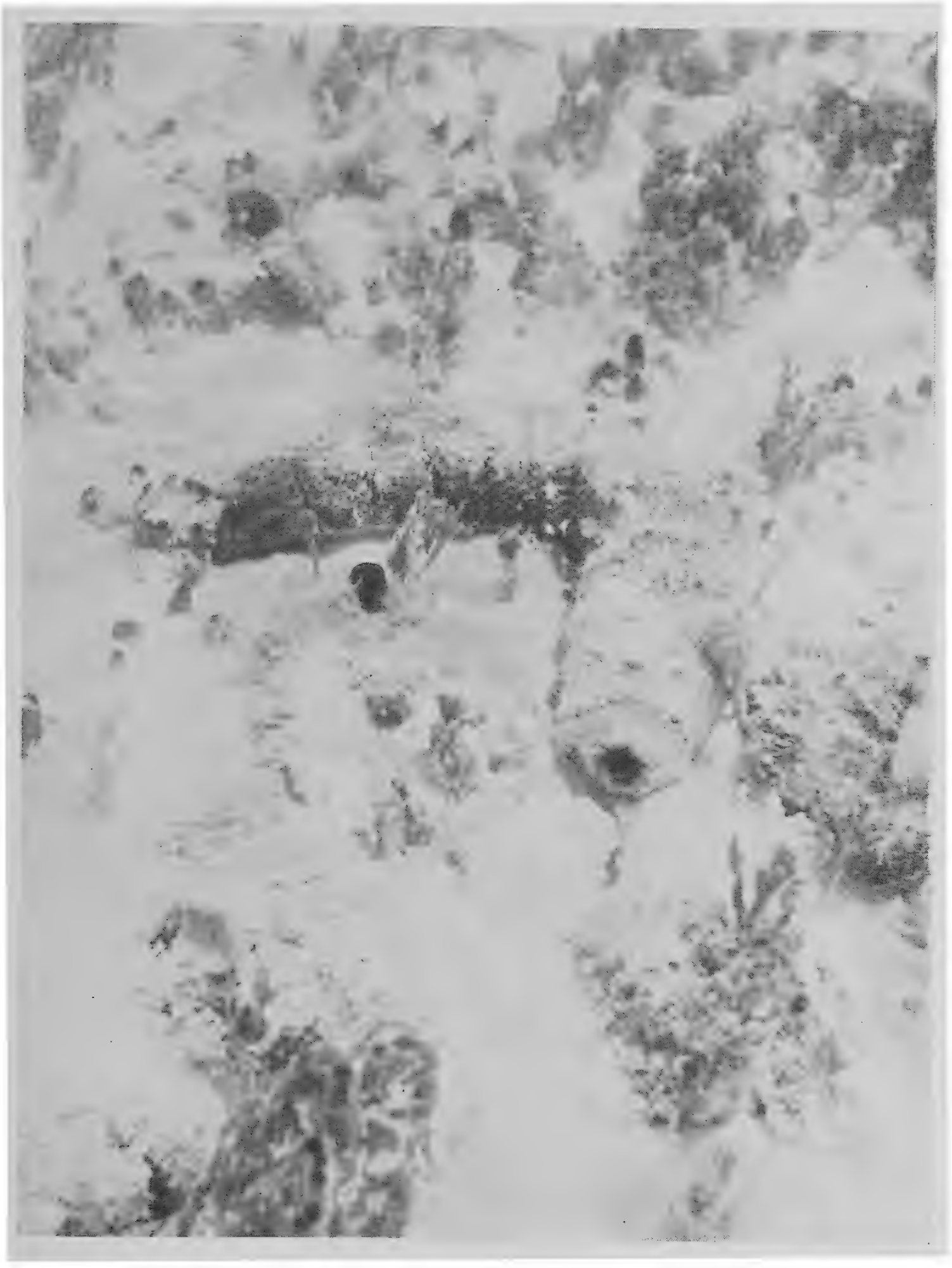

FIG. 13. Holothurian and algae on rock bottom, North Bimini Harbor. Water depth is about 1 meter.

FIG. 14. "Coral patch", North Bimini Harbor. Water depth is about 1 meter.

result of the high and variable salinities encountered in this region. It was not possible to evaluate the role of sediment type, which actually might be quite important. Living Podocopa and Platycopa are fairly common. Dead ostracodes are extremely abundant. The abundance of dead ostracodes is attributed to the relative scarcity of other organisms with calcareous parts living in this area. Some podocopid species which are present in abundance in the sediment are restricted to this region; other species abundant elsewhere are absent here. This distribution is also considered the result of high and variable salinities (see section on "Salinity").

Oolite facies (VI): The term oolite sand is loosely used in this paper to include calcium carbonate coated faecal pellets as well as spherical grains with well developed concentric structures.

Two oolite bores are a minor part of the oolite sands in the Bimini area. Level oolite sand areas are commonly coated with organic detritus which makes them darker than the oolite bores. They also support more vegetation than the bores. Identification of these sands as oolite requires close examination of the sediment. They are not distinguishable from bioclastic sands on aerial photographs as are the bores.

Sediments belonging to the oolite facies are characterized by being extremely well sorted; the diameter of most grains lies within the 124–248 micron range. The dry (and

wet) bulk density of oolite sand is higher than that of other sands in the vicinity of Bimini (Figs. 24, 25). The organic carbon content of oolite sand is lower than in other sediments in this region. However, a film of organic detritus is not uncommon on the sediment.

Living and dead ostracodes are virtually absent from the area covered by oolitic sands. The influence of the oolite sands on the distribution of ostracodes is especially notable in the submarine area around the eastern end of South Bimini. In this region ostracodes are abundant in the pitted and chalky bioclastic sediments but are absent or extremely rare in the adjacent oolitic sands.

The reason for the rarity of ostracodes in the oolite sands is not definitely known. Vegetation is sparse in this region, and the organic carbon content of these sands is lower than in the other sediments in the Bimini vicinity, so it is possible that food supply may be the limiting factor. Organic detritus is present on much of the oolite sediment, and the vegetation, although sparse, possibly occurs in sufficient quantities to support more ostracodes than are present in these sands.

In the Bimini vicinity, except for the two bores shown on the map insert, which probably are shifting, the sand has been somewhat stabilized by sparse vegetation; ripple marks and other evidence of shifting were not observed. Therefore, in this area

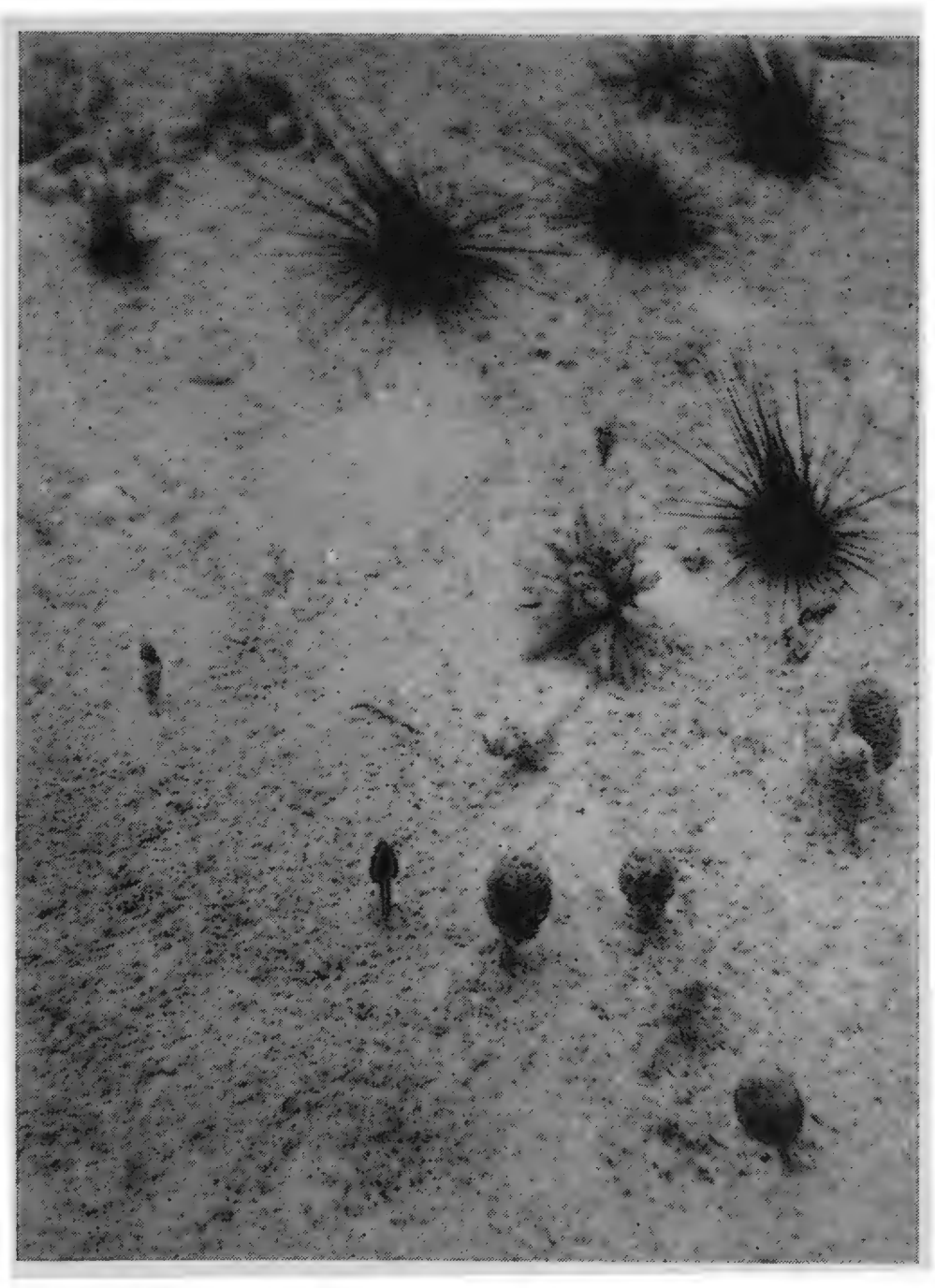

FIG. 15. Echinoids and algae on rock bottom, North Bimini Harbor. Water depth is about 1 meter.

sand movement is not likely to be a major environmental factor influencing the distribution of ostracodes.

Six myodocopid ostracodes were isolated in glass vials containing oolite. After 23 days all ostracodes were alive and several living young had been produced. Although the data are too few to be conclusive, it does suggest that oolite is not inhibiting.

FIG. 16. Dense *Thalassia*, south of South Bimini. Water depth is about 5 meters.

The writer from observing the behavior of ostracodes in the laboratory has come to the conclusion that physical properties of sediment are extremely important to benthonic ostracodes who crawl on, or burrow into, the sediment. The interstices between grains of Bimini sediments were too small to accommodate an ostracode, so that in order to burrow the animal had to force its way into the sediment. Although the ostracode does this partly by moving grains to the rear with its appendages, most of the forward movement is accomplished when the animal using its carapace as a wedge forcing it through the sediment by pulling and pushing on grains of sediment. The ability of an ostracode to burrow therefore depends both on its strength and the resistivity of the sediment to displacement.

Oolite is the densest sediment in the Bimini area. It is possible that ostracodes avoid the oolite area because of burrowing difficulties. See preliminary experiments suggesting that ostracodes may prefer to burrow in less dense sediment, Kornicker (1957a).

With the exception of the oolite, which seems to be unfavorable for ostracodes, the type of sand in the Bimini vicinity did not appear to exert any marked influence over areal ostracode distribution.

Grass, Rock, and Open Sand.—The bottom in the Bimini vicinity is almost equally divided into rock areas, open sand areas, and grass areas (Fig. 26 folded chart). *Thalassia*

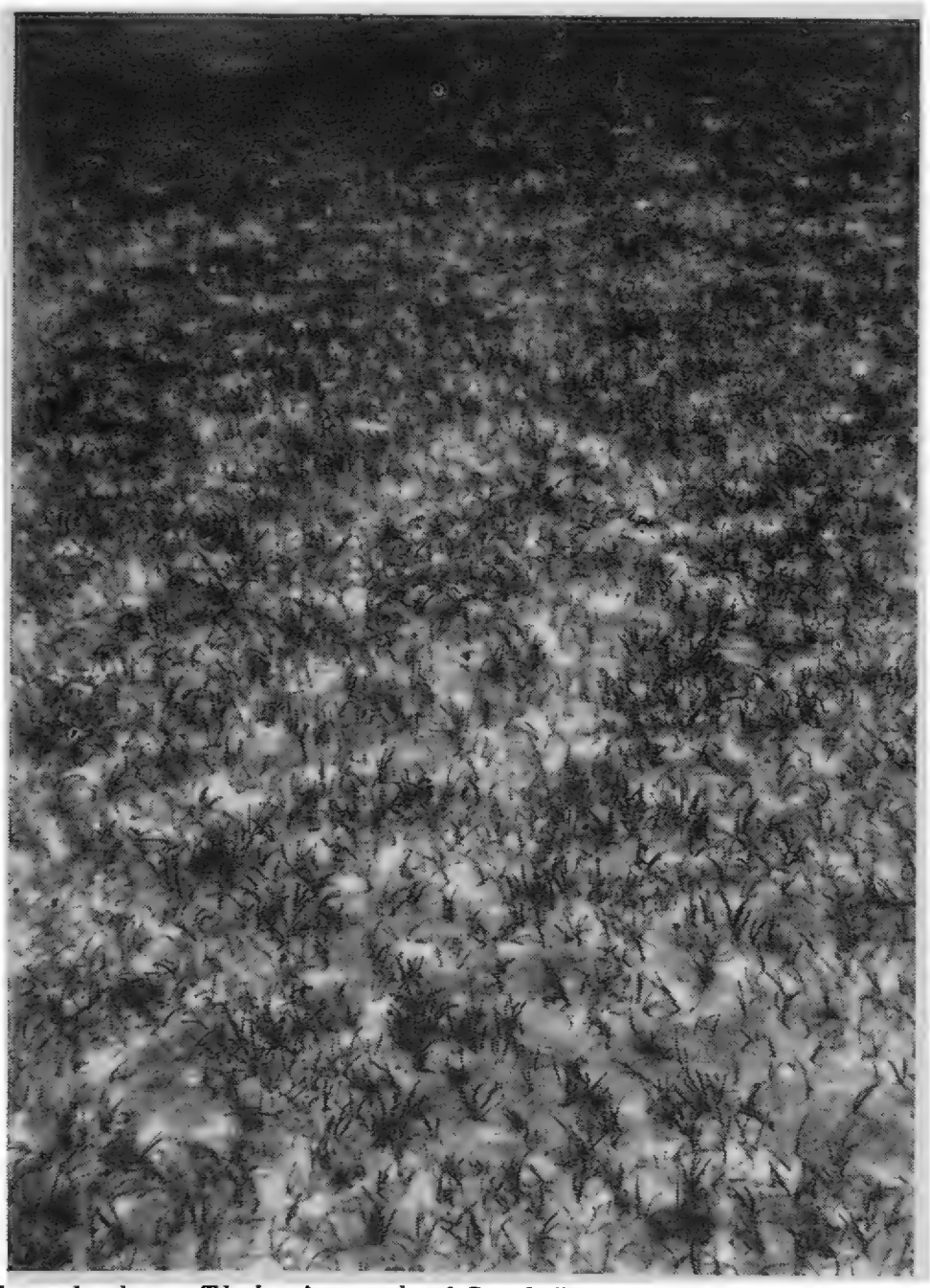

FIG. 17. Moderately dense *Thalassia*, south of South Bimini. Water depth is about 2 meters.

FIG. 18. Sparse *Thalassia*, south of South Bimini. Water depth is about 2 meters.

FIG. 19. Community living on sand-covered rock. Water depth is about 6 meters.

FIG. 21. Sea fans and *Madrepora* on rock bottom near Turtle Rocks. Water depth is about 7 meters.

FIG. 20. Coral heads and rock ledges on rock bottom near Turtle Rocks. Water depth is about 7 meters.

FIG. 22. Sea whip in foreground is characteristic of the rock bottom near Crossing Rocks. Depth of water is 6 meters.

FIG. 23. Note the snail *Cyphoma*, which is a common inhabitant of sea whips near Crossing Rock. Water depth is 6 meters.

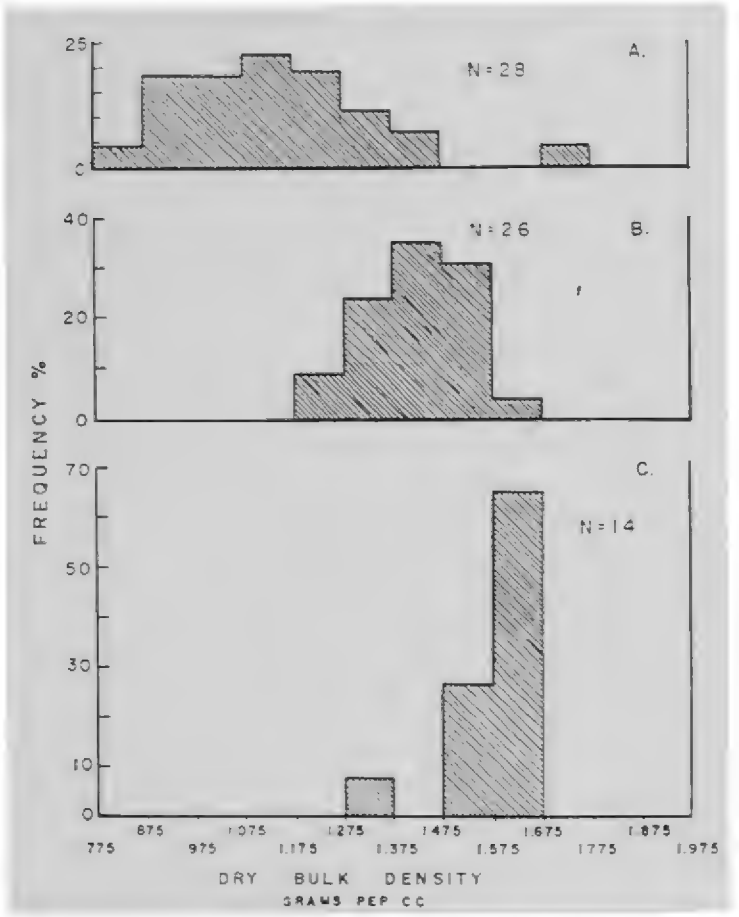

FIG. 24. Comparison of dry bulk density of sediment from "A" chalky facies, "B" glazed facies, and "C" oolite facies.

is by far the dominant vegetation and mostly grows either in small patches or covers larger areas where it is usually sparse.

Before the investigation the writer thought that large variations in ostracode distribution and abundance would be found among the different bottom types. Therefore, sampling was conducted so that each bottom type was sampled in all areas. Statistical consideration of the data did not produce significant differences with the exception of the platform area west of North Bimini, where both the living and dead ostracode abundance varied directly with the estimated areal coverage of the sampling locality by flora and fauna (P less than 5). The flora and fauna were principally confined to the rock bottom and practically absent from the wave-agitated sand areas (Fig. 27).

The writer has no explanation for not finding larger variations in ostracode content on different bottom types in the other areas. Perhaps it indicates an abundance of food in all areas. Detailed sampling may bring out subtle differences masked by the present sampling procedure.

INFLUENCE OF SALINITY AND TEMPERATURE ON OSTRACODE DISTRIBUTION

Salinity.—Typical salinity values (in parts per thousand) reported by Turekian (1957) for the Bimini area are listed in Table 2. These salinities were obtained during the spring mostly under dry conditions. After a heavy rain the regions with limited intercourse with the open sea experience marked lowering of salinity. For example, the salinity just below Mosquito Point in North Bimini harbor decreased from about 39 parts per thousand to 30.8 following a rain (Turekian, 1957).

The salinity fluctuation of the Florida Straits and Great Bahama Bank water in the vicinity of Bimini was very small. In North Bimini harbor the fluctuation in salinity was somewhat greater, but in all three regions the salinity remained within the 30 to 40

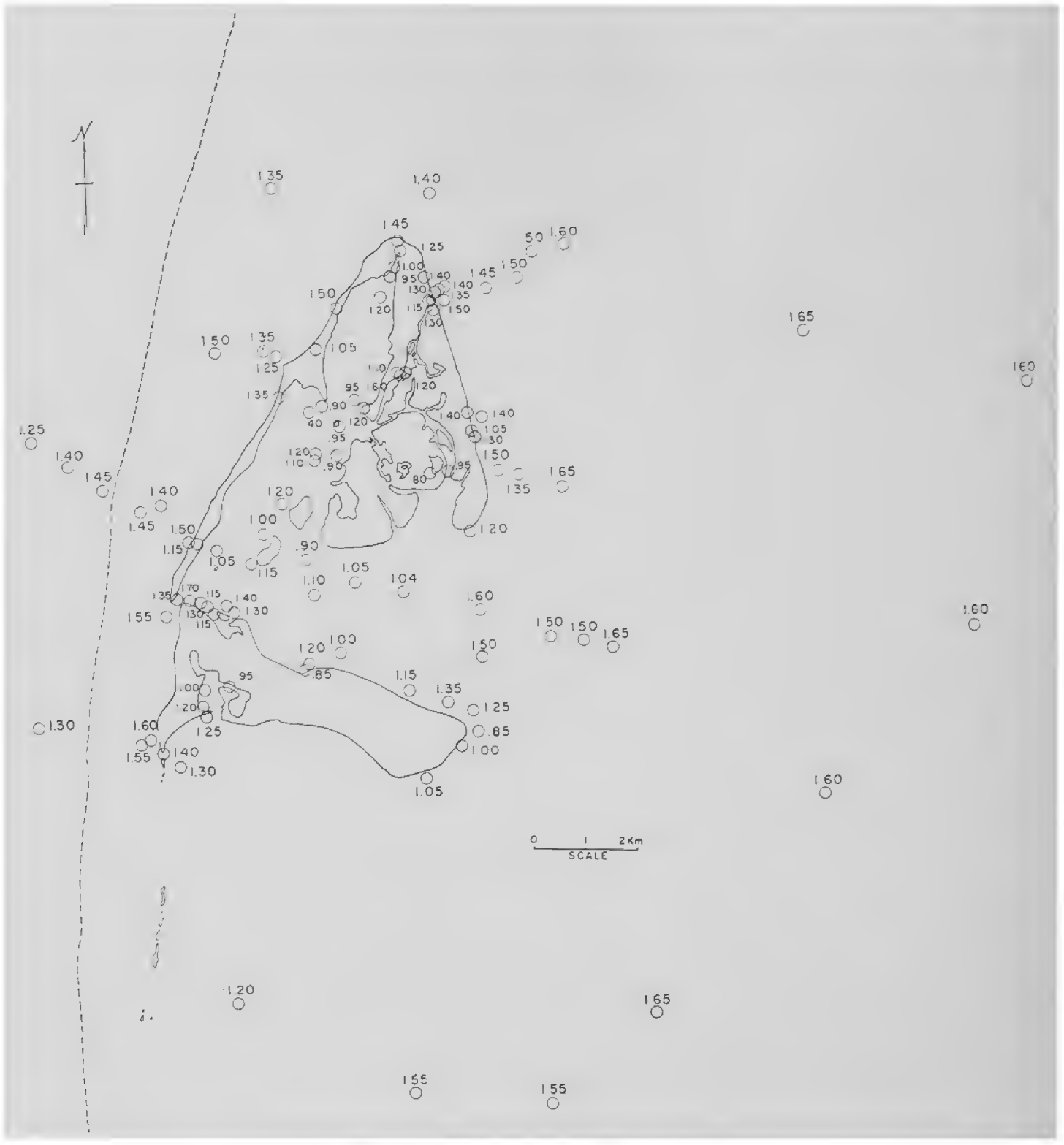

FIG. 25. Dry bulk density of sediment in vicinity of Bimini (grams per cc.).

parts per thousand range considered by Hedgpeth (1951) to include normal marine water. Fluctuation within this range generally has relatively little effect on the distribution of fauna (Dahl, 1956). Ostracode communities which inhabited these areas in the Bimini region contained essentially the same species, and variation in ostracode abundance does not seem attributable to these small differences in salinity.

The movement of water in and out of North Sound during change of tides is restricted because of its geographical position at the end of the harbor and because of lateral land projections and a rock sill athwart the current at its lower end. In June the water during periods of low rainfall became highly saline (more than 40 parts per thousand), and after a considerable amount of rain the salinity dropped to about 31–35 parts per thousand or lower (Turekian, 1957). The steep salinity gradient encountered here or possibly the high variability of the salinity seemed to have considerable effect on the faunal and floral communities inhabiting the region. Echinoderms were absent, and

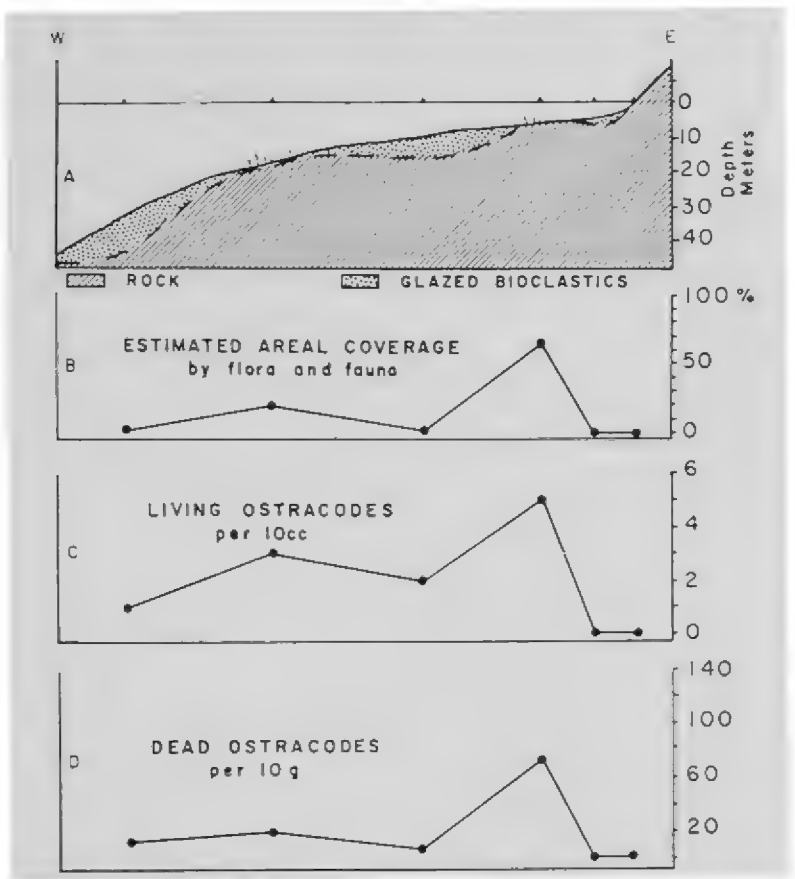

FIG. 27. Platform Area West of North Bimini.
A. Cross-section showing distribution of the sediment.
B. Estimated areal subsurface coverage by flora and fauna.
C. Number of living ostracodes per 10 cc. sample.
D. Number of dead ostracodes per 10-gram sample.

TABLE 2

Salinity of Water in Bimini Area

	Salinity
Florida Straits (near Bimini)	35.85–35.92
Great Bahama Bank (near Bimini)	37.50
North Bimini Harbor	36.10–39.40
North Sound	40.00–46.50
Cavelle Pond, South Bimini (1 sample)	31.52

corals as well as most sponges were restricted to the lower end where normal marine salinities occurred (Fig. 28–29).

The ostracode population also experienced a change in this region (Fig. 30). The genus *Bairdia* which was common in all other environments in the Bimini area did not occur in the upper part of North Sound. *Loxoconcha dorsotuberculata* (Brady) also was restricted to the lower end. *Loxoconcha levis* (Brady) was collected only in the upper part of North Sound. Another species (*Hemicythere* sp.) was also restricted to the northern end. The last two species were not collected alive. *Hemicytere* sp., however, often contained appendages which indicates that the specimens died recently. The Myodocopa also seemed restricted to the less saline southern part.

The sediment in the northern part of the Sound contained an abundance of empty ostracode carapaces. These could not be accounted for by an abundance of living ostracodes. An explanation for this favored by the writer is that the absence of other sediment-forming organisms such as corals and the alga *Halimeda* permitted the empty ostracode carapaces to form a large part of the sediment.

Cavelle Pond is a small pond on South Bimini (Fig. 1). It is almost bisected by a

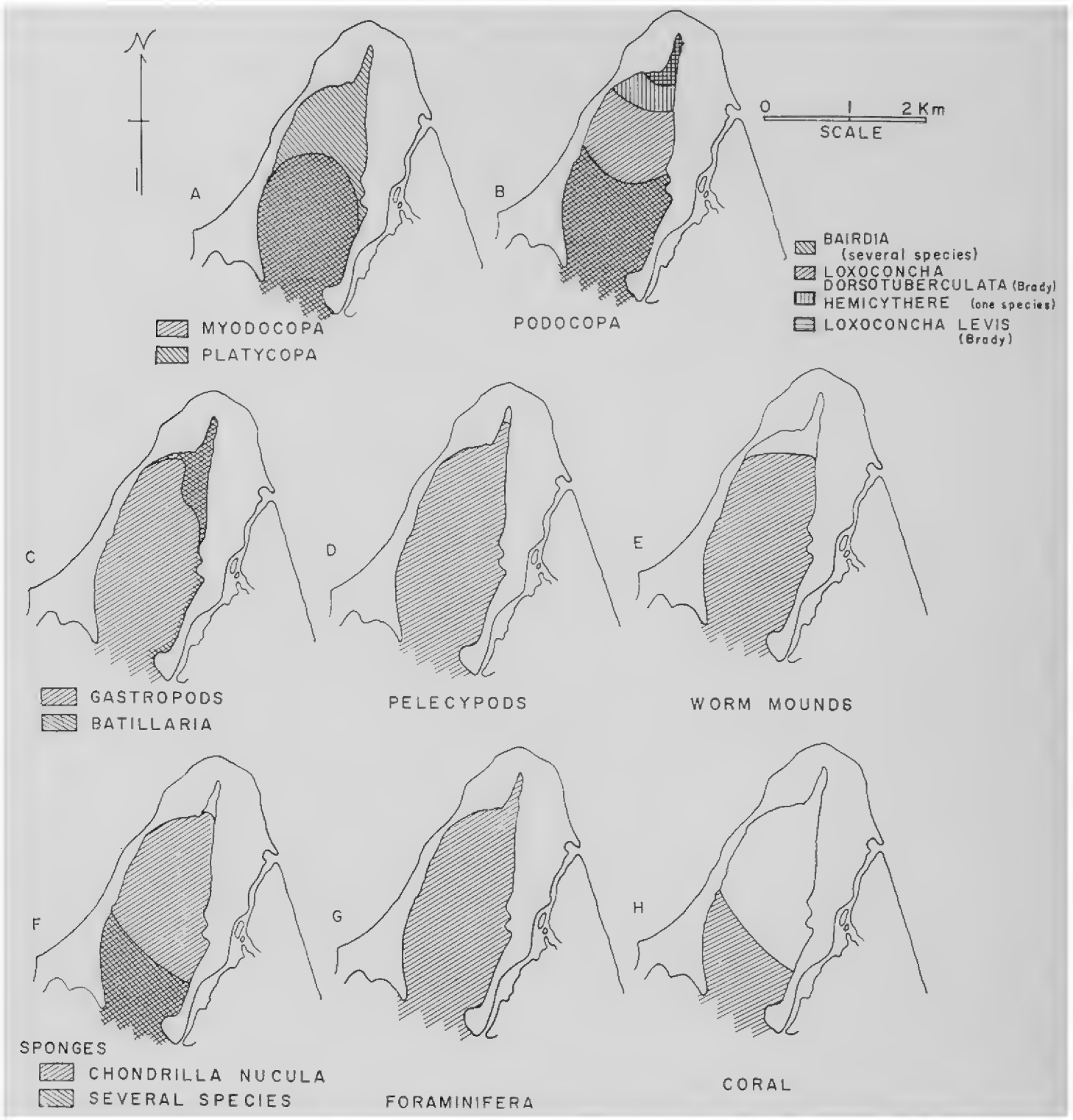

FIG. 28. Faunal ranges in North Sound.

north-south trending mangrove spur. The two halves of the pond are connected at the northern end by a shallow stream which has a rock bottom on which corals grow. Each section of the pond has a sediment substrate which supports a luxuriant crop of vegetation.

The only salinity determination available for this pond is 31.5 parts per thousand, obtained from the center of the western section of the pond (Turekian, 1957). Interchange of water during tidal change is quite rapid, and it is probable that the waters in at least the western section are normally marine, although it is not unlikely that after a heavy rain the salinity falls below 30 parts per thousand.

The dominant ostracode genus present in the sediment is *Cyprideis*, a known brackish water form (Brady, Crosskey, and Robertson, 1874; Sohn, 1951; Swain, 1955). Also abundant in the sediment are valves of the pelecypod *Anomalocardia cuneimeris* which is a recognized estuarine (poikilohaline) species (Hedgpeth, 1953, p. 178). Neither of these forms which were abundant in the sediment were found alive.

In Cavelle Pond many species of dead ostracodes in the sediment are not living in the

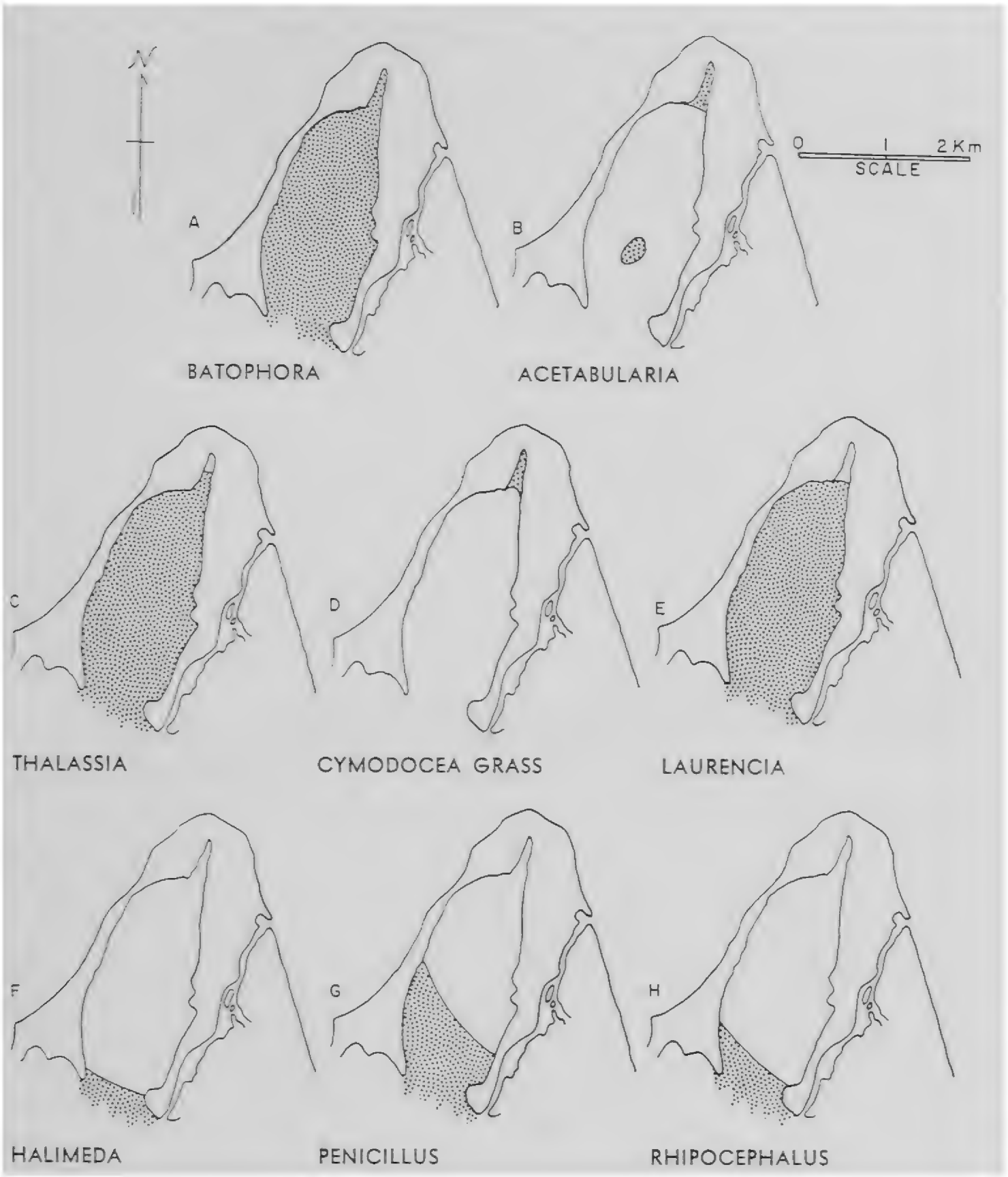

FIG. 29. Floral ranges in North Sound.

pond at the present time. Marine forms are living in the pond, whereas estaurine forms compose a large part of the sediment. An examination of the older maps of the region revealed that Cavelle Pond was once closed off from the sea. The earliest map reviewed showing a connection between Cavelle Pond and the sea was the Naval Air Pilot, 1940, H. O., No. 194. United States Navy Department. Hydrographic Office. p. 198. Inhabitants of Bimini recall that the pass connecting Cavelle Pond with the sea was excavated in an attempt to reduce the number of mosquitoes breeding in the brackish water of the pond.

Although living ostracodes belonging to the suborder Myodocopa were abundant around Bimini, their remains were absent from the sediment probably because of poor preservation of the carapace, which usually soften after death of the animal. With the exception of the North Sound and Cavelle Pond areas, species belonging to the sub-

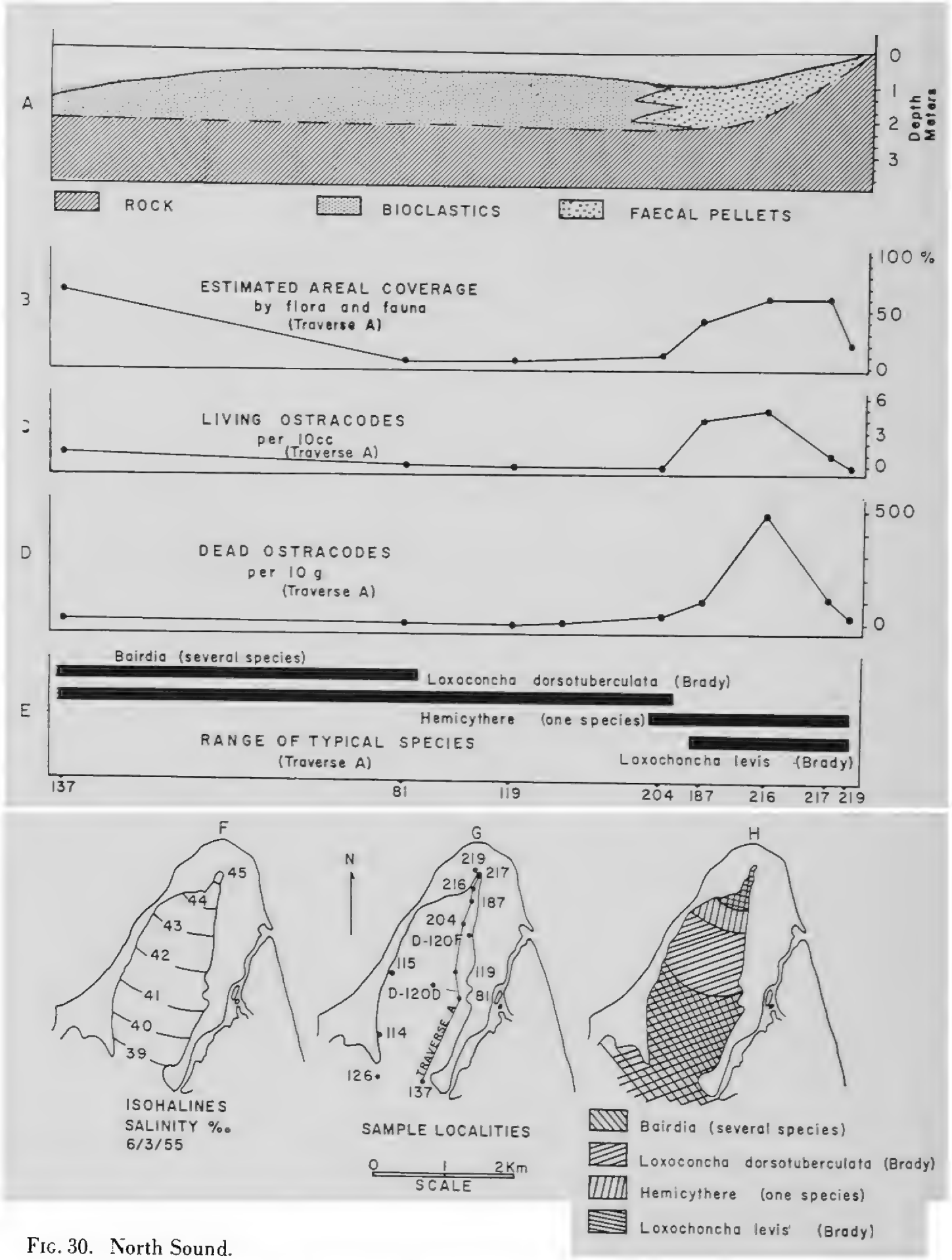

FIG. 30. North Sound.
A. Cross section showing distribution of sediment.
B. Estimated coverage of subsurface by flora and fauna.
C. Number of living ostracodes obtained in 10 cc. sample.
D. Number of dead ostracodes obtained in 10 gram samples.
E. Range of typical species along Traverse A (see part G for location of Traverse A).
F. Salinity isohalines in North Sound. Data partly from Turekian (1957).
G. Sample locality map.
H. Map showing distribution of typical species in North Sound.

orders Podocopa and Platycopa represented by many empty carapaces in the sediment were also collected alive during the periods in which this study was made.

Temperature.—Daily temperature variations in the Bimini vicinity were only a few

degrees (Turekian, 1957), and under normal conditions this difference is not likely to have any effect on ostracode distribution. Occasionally, however, unusually cold winter temperatures have been encountered. For example, Dr. Louis A. Krumholtz (personal communication, 1956) recorded a temperature of 14° C. in North Bimini harbor on January 12, 1956. At this time fish were killed by the cold water of the harbor. The effect of this low temperature on the ostracodes of the region is not known, but it is possible that the absence of living *Hemicythere* sp. from North Sound was a result of the low temperature of the previous winter. The carapaces of this species, which in many instances still contained appendages, were abundant in the sediment.

Influence of Water Color and Phototaxis on Ostracode Distribution

The waters of North Bimini harbor often were greenish-yellow when viewed from a distance. This was especially noticeable during ebb tide where the harbor water entered the blue waters of the Gulf Stream. Yellow color may be due to a trace of organic compounds which absorbs blue and near ultraviolet light (Harvey, 1955) and may be derived from mangroves or marine vegetation. The color, as determined by a Taylor Color Comparator (Table 3), which probably did not differentiate subtle color variation, did not seem to have any influence on ostracode distribution.

Table 3

Water Color and pH

Location	Water Color*	pH*
Northern end North Sound	15	8.0
Center North Sound	0–5	8.2
Big Mangrove Cay	0–5	8.2
Southern end North Sound	0–5	8.2
Center North Bimini Harbor	0–5	8.1
Tokas Cay	0–5	8.2
Southern end North Bimini Harbor	0–5	8.1
West side Cavelle Pond	0–5	8.2
East side Cavelle Pond	0–5	8.2
South of Cavelle Pond	0–5	8.2

* All samples were obtained between the hours of 6:00 A.M. and 9:00 P.M. during June, 1956.

In shallow water near land areas a considerable number of particles which reflect light upward are usually in suspension. The amount of reflected light is also affected by the substrate; open sand reflects more light than either grass or uneven rock. The amount of light reaching the bottom probably has an influence on ostracode distribution. Ostracodes seem to be either negatively or positively attracted to light (see Kesling, 1951). The response to light of specimens of Myodocopa collected by dragging a net through a *Thalassia* patch in North Bimini harbor was observed in a petri dish for one hour and 35 minutes. The net response of this population to light was positive (Fig. 31).

Influence of Dissolved Oxygen and pH on Ostracode Distribution

Dissolved oxygen in the waters of Cavelle Pond and North Bimini harbor was determined using the Winkler procedure (Table 4). The waters were found to be sufficiently aerated, and it is improbable that ostracode distribution was affected directly by oxygen.

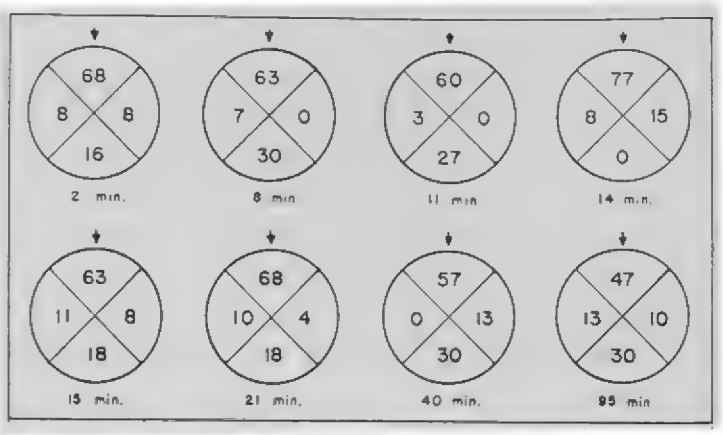

FIG. 31. Response of Myodocopa to light. Petri dish was rotated before each observation. Light source was microscope lamp. Sample of ostracodes was obtained from *Thalassia* patch in North Bimini harbor. Community contained *Sarsiella truncana* (13), *S. carinata* (11), *S. gigacantha* (5), *S. punctata* (3), *S. capillaris* (3), *Philomedes multichelata* (1), *P. paucichelata* (8), *Rutiderma dinochelata* (1), *Asteropteron monambon* (2).

TABLE 4

Dissolved Oxygen Content of Waters

North Bimini Harbor*

Oxygen ml/L	Water Temperature C.	Time	Air Temperature C.	Date ....
			22.9	11/10/56
3.69	23.5	10:30	24.4	....
3.93	24.1	11:30	24.9	....
			23.4	....
4.64	25.7	1:30	24.7	....
5.25	....	4:45	24.5	....

Cavelle Pond, South Bimini**

Oxygen ml/L	Water Temperature C.	Time	Air Temperature C.	Date ....
5.03	25.2	2:00 P.M.	....	11/6/56
5.16	....	2:15	....	....
4.99	24.9	2:20	25.1	....
5.30	....	2:30	....	....
5.38	24.7	2:45	—	....

* Location: east of Lerner Marine Laboratory, about 22 meters from shore, water about 1 meter deep. High tide was at 2:30 P.M.

** Location: about 30 meters within the entrance of Cavelle Pond, water about 1 meter deep. High tide was at 12:00 M.

The pH variation in the Bimini vicinity was small and did not appear to be a factor directly influencing ostracode distribution (Table 3). This conclusion coincides with observations which were made in other areas by Tressler and Smith (1948) and Benson (1955).

INFLUENCE OF ORGANIC CARBON AND ORGANIC DETRITUS ON OSTRACODE DISTRIBUTION

Organic detritus.—A gelatin-like film containing fragments of shell debris and plants, unicellular algae, and diatoms (Fig. 32) formed a tan-colored coating on the submarine sediments in the vicinity of Bimini (Fig. 33). A simple experiment in which water from North Bimini harbor was pumped into a settling tank demonstrated that this material was also suspended in the water (Fig. 34).

Organic detritus is considered a basic food for benthic fauna (Dexter, 1944). Yonge (1953) questions the actual food value of detritus and states, ". . . possibly its major

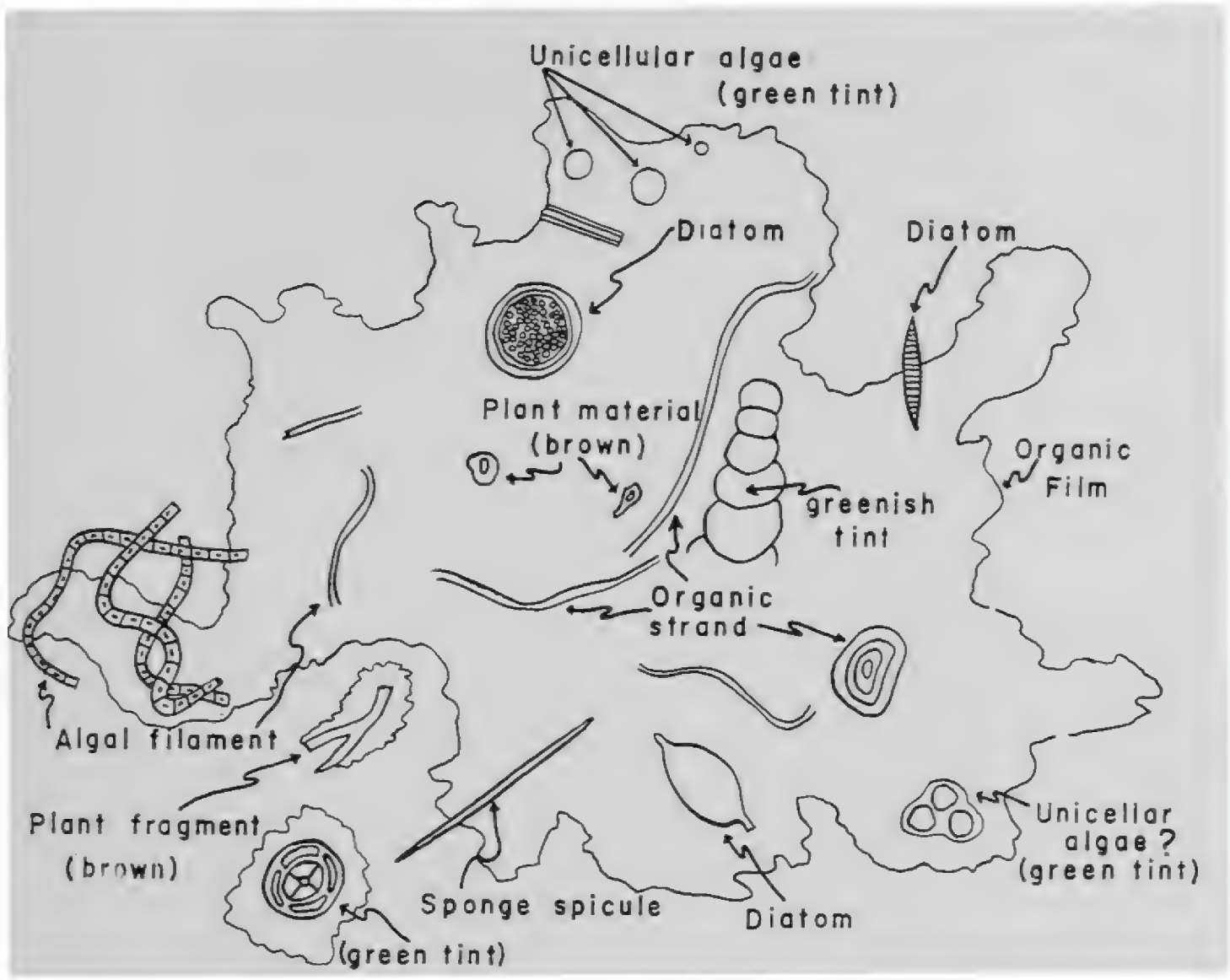

FIG. 32. Organic detritus (sketched under high magnification).

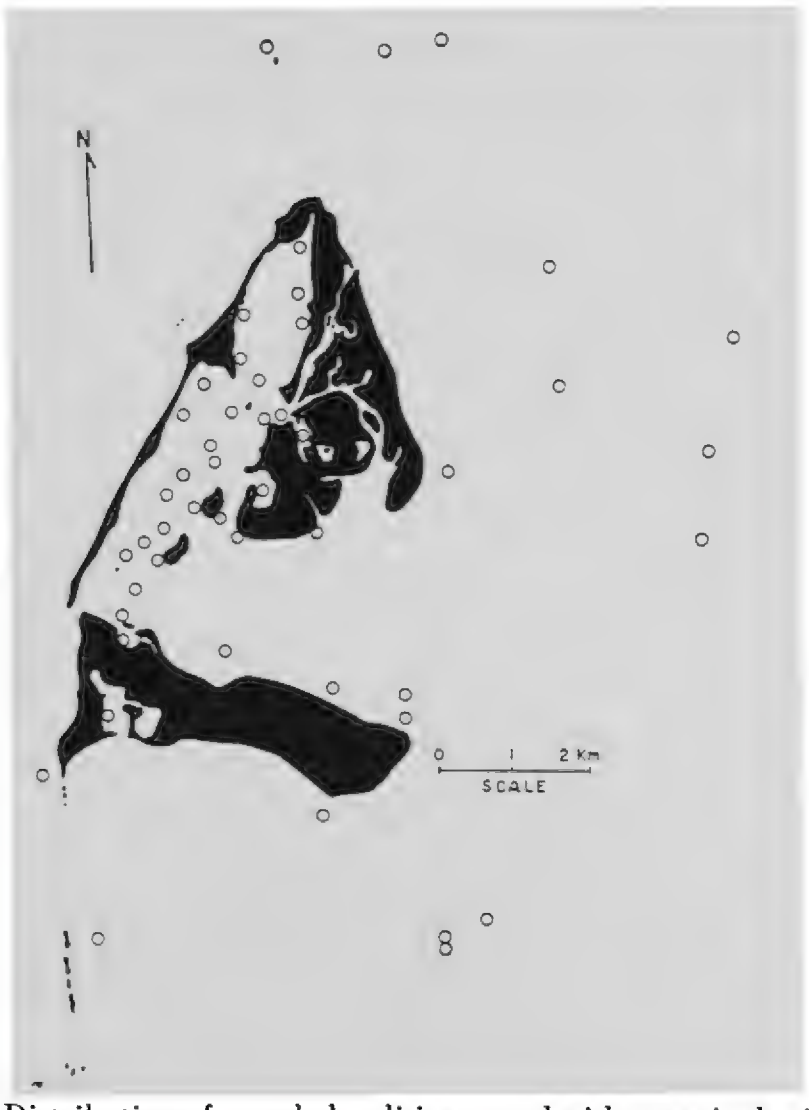

FIG. 33. Distribution of sample localities coated with organic detritus.

FIG. 34. Photograph of sand on bottom of small tank through which 3,000 gallons of water were passed at the rate of 2/3 gallon per minute. In the top part of the photograph the organic detritus which settled from the water has been removed to expose clean sand. The contrasting dark color in the lower part of the photograph is the result of organic detritus accumulation.

importance may be as a culture medium for Protozoa and bacteria." Cannon (1934) concludes, after studying the feeding mechanism of *Cypridina antarctica* and members of the subfamily Philomedinae, that these ostracodes probably feed on minute detritus. Klugh (1927) found that several fresh water species ingested both algae and detritus but did better on algae.

Hoff (1942) states, "The foods of few species (of ostracodes) have been studied in detail, although a study of food habits might have some bearing on problems of distribution." Very little has been added to knowledge concerning the food habits of ostracodes since Hoff made the statement quoted above. It seems probable, however, that at least some of the ostracodes in the Bimini vicinity feed on organic detritus.

The presence or absence of organic detritus seemed dependent to a large extent on current action. In shallow areas where the sand was in almost continuous action, organic detritus was rare and probably had been removed by currents. Ostracodes were usually rare in these sands, but this was probably because agitated sand is an unfavorable habitat rather than because of the lack of detritus. Extensive areas of oolitic sand which were almost barren of ostracodes were coated with organic detritus.

Organic Carbon.—Sediment from creeks flowing through mangrove swamps on East Bimini were found to be relatively high in organic carbon (1.39 to 2.90 percent) (Fig. 35). Many of these sediments were dark in color, emitted an H_2S odor, and contained fragments of mangrove leaves. Ostracodes were rare in these sediments.

Sediment within North Bimini harbor and most of North Sound contained the next highest organic carbon content (0.44 to 1.00 percent; average 0.74 percent). The lowest organic carbon content was encountered in the sediments on the outer side of the islands (0.39 to 0.61 percent; average 0.49 percent).

Within small areas, such as North Bimini harbor, the organic carbon content of the sediment was uniform, even though the amount of visible vegetation varied at the sample stations. Perhaps this is the reason for finding in this study about the same number of ostracodes living in open, nonshifting sand areas as in neighboring vegetated areas.

Influence of Current Velocities on Ostracode Distribution

The highest current velocity in the area caused by tides was encountered at the entrance of North Bimini harbor, where the velocity reached 1.2 meters/second during ebb tide. This dropped to 0.16 meters/second outside the entrance. Within the harbor the highest current velocities occurred within the main channel. A measurement of 0.3 meters/second was made in this channel about 1.5 kilometers from Entrance Point. In the northern part of the harbor the current velocities were very low (0.01 meters/second).

South of South Bimini, except close to shore where the crescent shape of the southern shore line created a low current velocity area, the current velocities approached those encountered in the main channel of the harbor. The highest velocity measured in this area was 0.5 meters/second, which occurred immediately above the crest of an oolite ridge. The restriction in the path of water flow created by this ridge caused an increase in current velocity. Velocities in about the same range as those south of South Bimini were obtained north of North Rock. Velocity measurements taken immediately to the east of Bimini, on the Great Bahama Bank, indicated low velocities in this area (maximum velocity recorded here was 0.18 meters/second).

A current velocity measurement of 0.2 meters/second was obtained west of North Bimini, between Paradise Point and Stepping Rocks. In this area waves were of greater importance as current producers than were the tides. Submarine ripple marks as well as the presence of winter berms on the beaches testified to the sediment-moving ability of the waves along the western shore of North Bimini.

Ostracodes were rare in the shifting sand area west of North Bimini and were absent in the channel at Entrance Point, where high water velocities probably disturbed the sediment. In the area between Turtle Rocks and South Bimini the current seems to keep the rock swept clean of sediment, and ostracodes were rare. From these observations the writer concludes that current velocities sufficiently high to stir the sediment may be a major factor in inhibiting the colonization of an area by ostracodes.

Most of the submarine environment included in this study was in shallow water less than seven meters deep.

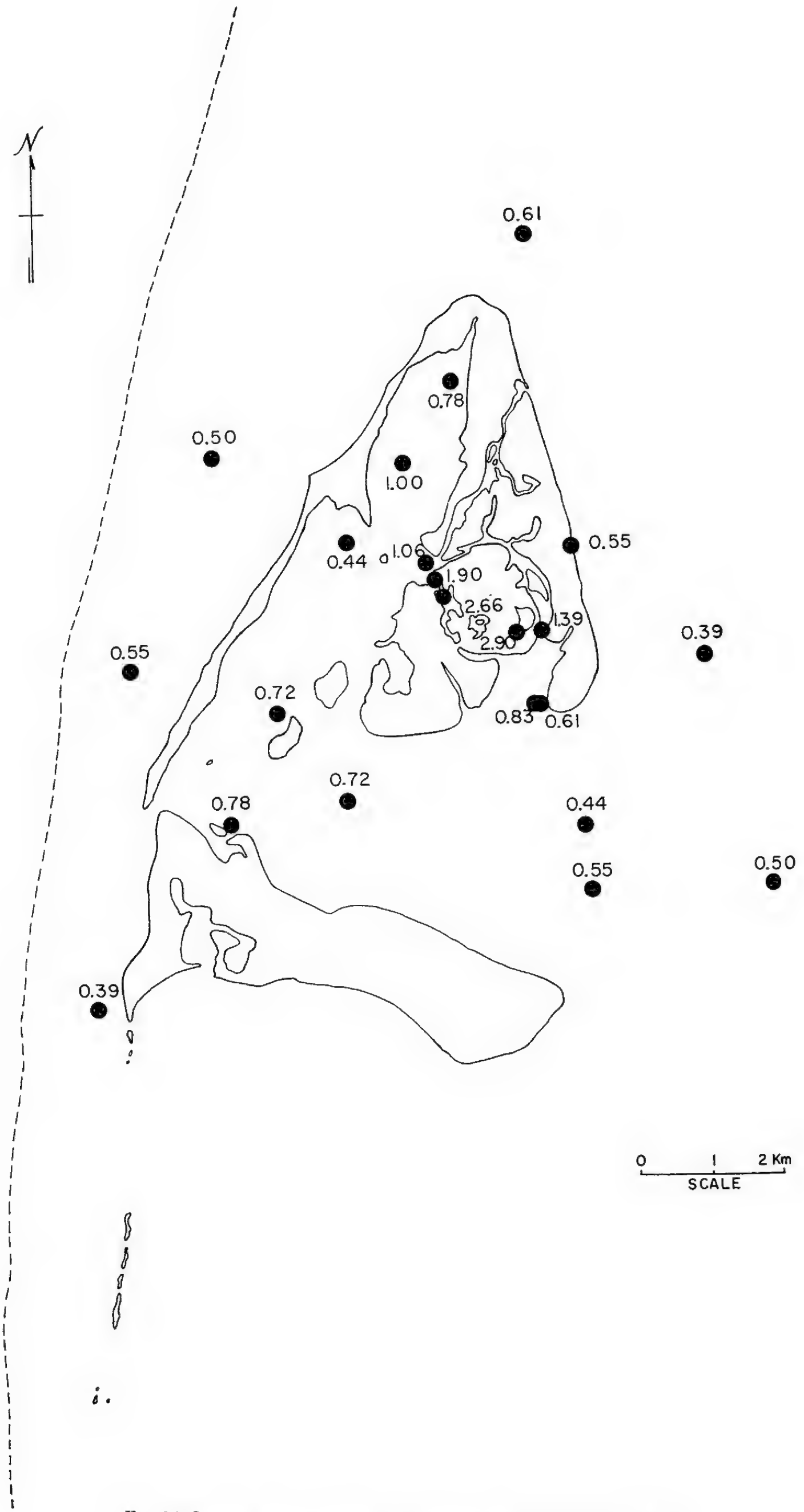

FIG. 35. Organic carbon content of the sediment (percent dry weight).

Systematics and Occurrences of Ostracode Species

Descriptions of Bimini ostracodes follow. These include diagnostic morphologic features only and are not complete descriptions. Morphological features are shown in detail in illustrations. When sexual differences are striking. or are important for identification, both sexes have been figured and described. Variations in taxonomically important appendages are mentioned in the diagnoses and usually are figured. Appendages (most frequently the furca) of juveniles have been figured as an aid to identification.

Numbers given to specimens are based on sample or station numbers used in the present investigation. Dissected specimens have been mounted in glycerin and protected with paraffin-sealed cover-glasses. Holotypes are dried shells. or. if these were not available, shells preserved in alcohol. Holotypes have been deposited with the Columbia University Geology Department.

Shells for measurement were selected at random from various growth stages. The drawings and photographs of ostracode morphology, Figs. 46–89. are collected at the back in an appendix for the convenience of taxonomists.

Suborder Myodocopa

Family Cypridinidae

Subfamily Cypridininae

Genus *Cypridina* Milne-Edwards

Cypridina squamosa subspecies *lerneri* Kornicker. new subspecies

(Figs. 47 1A-B; 48. A-D: 49. A-E)

Diagnosis: The shell is elliptical in lateral view, with protruding postero-ventral corner. The antennal sinus is fairly deep and the rostrum prominent. A cluster of muscle scars occurs near the center of the shell. Maximum shell height is posterior to the middle.

The adult furca bears eight claws; the fourth claw is smaller than the second and fifth; the second claw is attached to the lamina without a demarcation line at its base. The second antenna has basal spines which are longer on the distal joints. The secondary branch of the second antenna bears two long and two short bristles on the proximal joint and one long bristle on the end of the distal joint. The seventh limb has 23 to 29 lateral setae.

Comparisons: The shell of *C. squamosa lerneri* is very similar to that of *C. squamosa squamosa* Mueller. *C. squamosa lerneri* is smaller than *C. squamosa*. A gravid female of *C. squamosa lerneri* (specimen number 247–3) measured 2.04 mm. whereas the female of *C. squamosa* reported from the Bay of Naples by Mueller was 3.3 mm. in length. *C. squamosa squamosa* bears six to seven claws on the furca. whereas the adults of *C. squamosa lerneri* have eight.

Remarks: It is possible that two female ostracodes from the Dry Tortugas identified by Tressler (1949, p. 335) as *C. squamosa* belong in the subspecies *C. squamosa lerneri*. Tressler's specimens have only seven furcal claws but, as these specimens were only 1.71 mm. in length, they may have been immature. The present study shows that immature specimens have fewer furcal claws (Fig. 48. A-C).

Shell measurements (in mm.):

Specimen number	Length	Width	Height
212–1 (holotype)	1.31	0.55	0.79
247–3*	2.04	------	1.40
656F	1.42	------	0.94
P–1	0.71	------	0.45
246–7	1.18	------	0.80
93	1.58	0.62	1.03
127–1	1.29	------	0.87
127–2	0.81	------	0.54
127–3	1.26	------	0.84
127–4	1.26	------	0.81
127–5	0.71	------	0.45
127–6	0.74	------	0.48
93–2	0.84	------	0.54
170	1.19	------	0.68
5306M	0.71	------	0.48

* Gravide female.

Material: Twenty-four specimens were obtained from bottom samples and one (a male) from a surface tow. Five specimens. including a male and a mature female, were dissected. The holotype is specimen number 212–1 (an immature specimen) which is illustrated in Fig. 47, la-b. Carapace form was the same in mature and immature specimens.

Occurrence: *Cypridina squamosa lerneri* was most abundant east of South Bimini (Fig. 36). Specimens were collected in waters having temperatures of about 29.2°C. and salinities about 37.5 parts per thousand. Substrate was calcareous sand, and usually algae and *Thalassia* were growing in the area. One male was obtained in a surface plankton tow in North Bimini harbor.

Subfamily Philomedinae

Genus *Philomedes* Lilljeborg

Philomedes multichelata Kornicker, new species

(Figs. 46, 3A-B; 50, A-E; 51, A-D)

Diagnosis: The shell is elliptical in lateral view, with a shallow but distinct anterior sinus. The surface of the valves contains closely spaced pits and muscle scars.

The furca is long, narrow, and triangular in outline, with five strong and nine weak claws. The first antenna bears, on the penultimate joint, a sensory bristle which has numerous setae on the outer edge of its flattened base. The second antenna bears non-spinose, natatory setae; basal spines are absent. The mandible has, on the ultimate joint, two strong claws, one small claw, and two bristles. The exopodite of the mandible bears two bristles. The seventh limb has about five setae and terminates in a claw-like process. The female is not known.

Comparisons: *Philomedes multichelata* is closely related to *Philomedes oblonga*

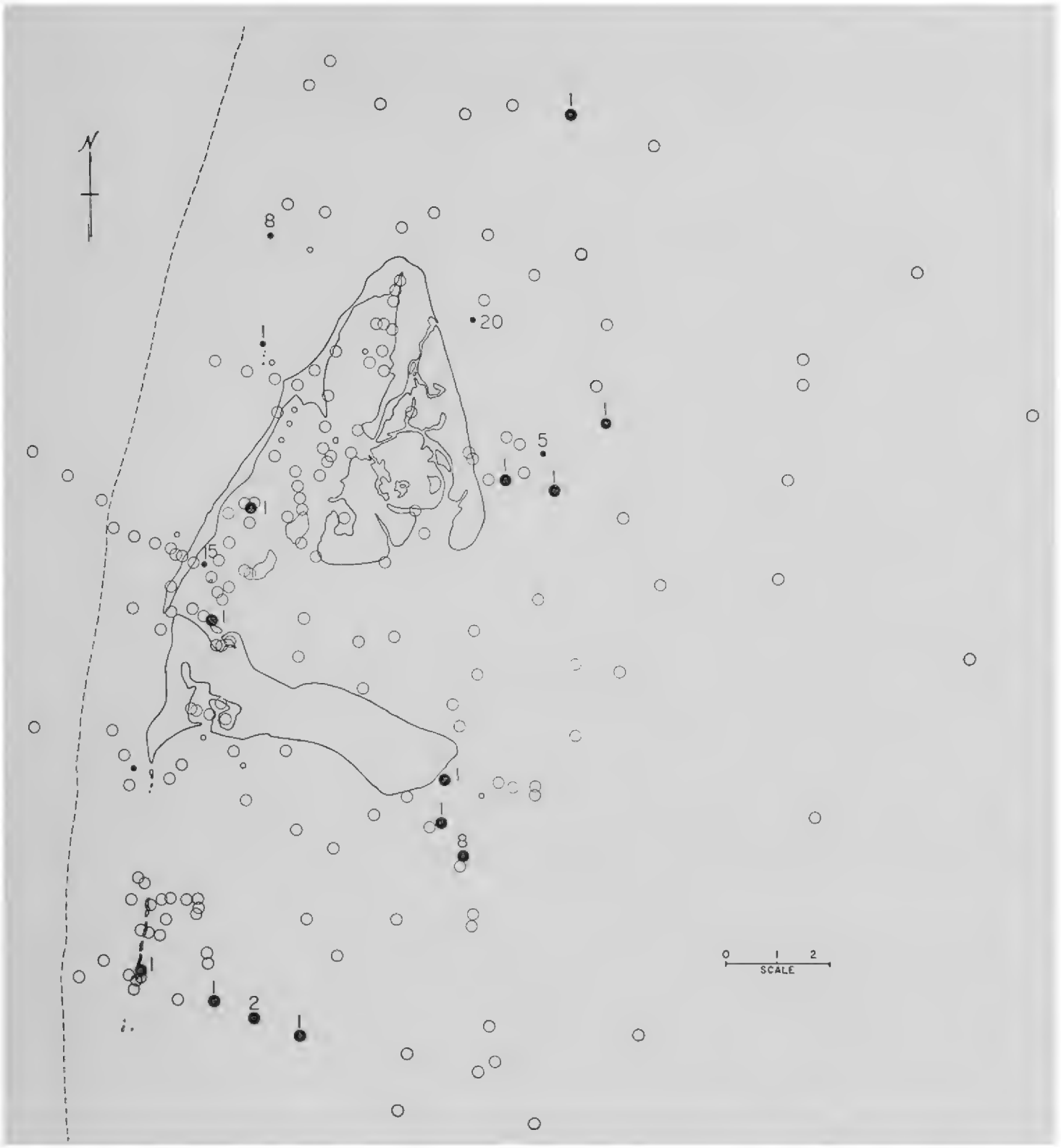

FIG. 36. Distribution of *Cypridina squamosa lerneri* Kornicker, new subspecies. Species was absent from samples shown as empty circles. Small circles represent trawl samples; large circles represent spot samples.

(Juday) Mueller, from which it differs in having 14 furcal claws, whereas, *P. oblonga* has only 10.

Shell measurements (in mm.):

Specimen number	Length	Width	Height
686Z–6 (holotype)	1.04	0.57	0.60
248	0.75	0.3	0.51
245	0.91	0.5	0.58
686Z–1	0.99	0.41	0.55
686Z–3	0.96	------	0.52
686Z–4	0.98	------	0.53
238	1.04	------	0.66 (approx.)

Material: Four specimens were obtained from bottom samples and several hundred from a single night surface tow. Four specimens (all males) were dissected. The holotype is specimen number 686Z-6, Fig. 46, 3a-b.

Occurrence: Two individuals were collected from the bottom southeast of South Bimini and one from the lagoon (Fig. 37). Several hundred specimens were collected around a night light suspended from the end of the Lerner Marine Laboratory dock in North Bimini harbor. The water at the time of collection had temperatures of 28.3° to 29.2°C. and salinities of 36.1 to 37.5 parts per thousand. The bottom was calcareous sand.

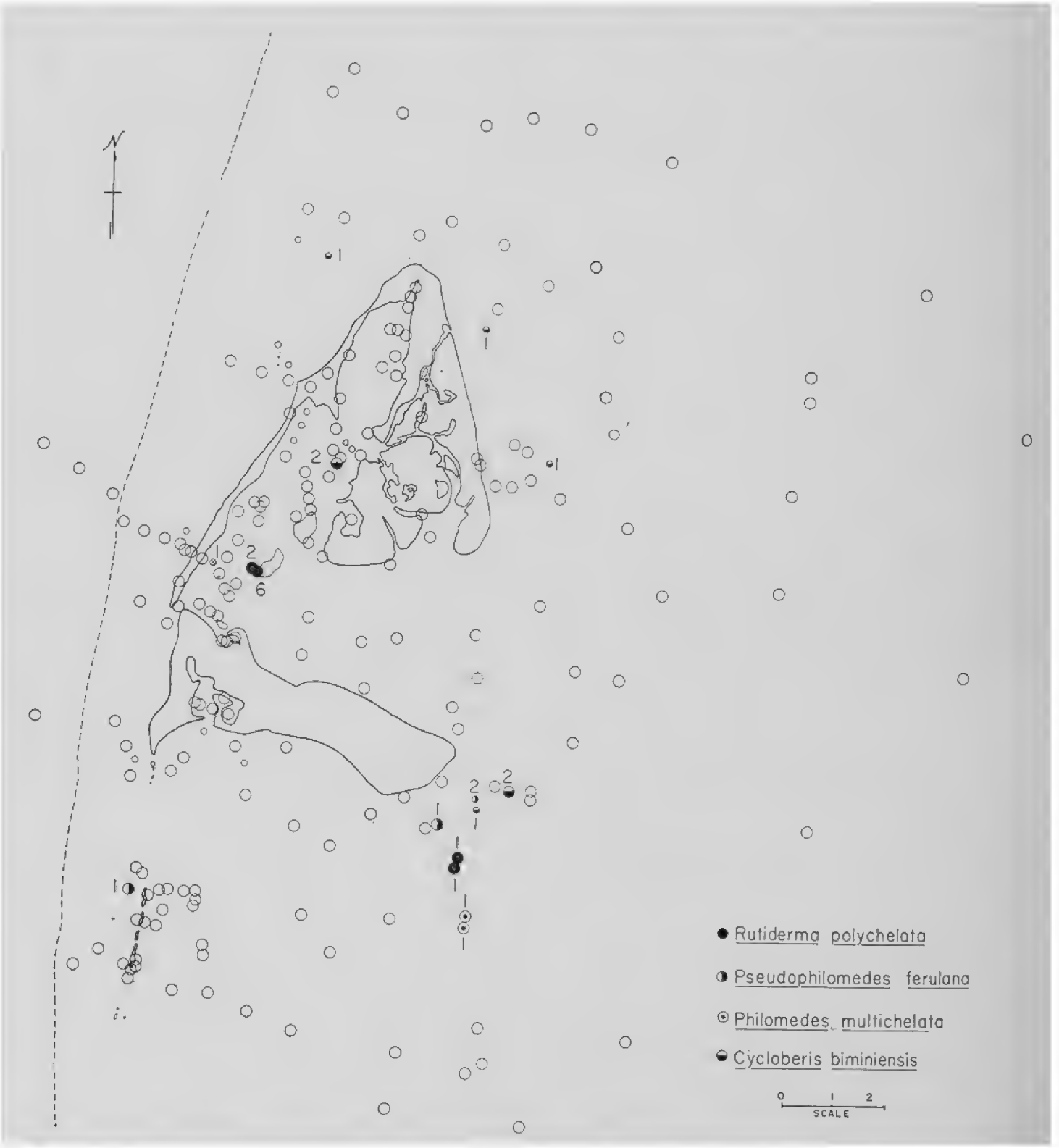

FIG. 37. Distribution of *Rutiderma polychelata* Kornicker, new species; *Pseudophilomedes ferulana* Kornicker, new species; *Philomedes multichelata* Kornicker, new species; *Cycloberis biminiensis* Kornicker, new species. Species was absent from samples shown as empty circles. Small circles represent trawl samples; large circles represent spot samples.

Philomedes lomae Juday

(Figs. 46, 7A–B; 52, A–E; 53, A–D; 86, A, E, I)

Philomedes lomae Juday, 1907, Univ. Calif. Publ. Zool., Vol. 3, No. 9, P. 141, Pl. 19, Figs. 1–6

Diagnosis: A process projects posteriorly from each side of the carapace, commencing at about the center. The antennal sinus is shallow but distinct. The surface of the valves is pitted.

The dorsal margin of the living ostracode is orange-red which fades rapidly after death, being no longer visible after a few months.

The furca contains six claws. The distal end of the fourth joint of the first antenna bears a sensory bristle which contains one thick and many fine setae. The secondary branch of the second antenna consists of three joints; the third joint is reflexed upon the second. A small sensory appendage which is ciliated on its outer extremity is on the distal end of the first joint of the mandibular polp. The terminal joint of the mandible contains one claw and three slender bristles. The female is not known.

Shell measurements (in mm.):

Specimen number	Length	Width	Height
115-Cl	1.24	0.44	0.75
215	1.18	0.34	0.73
92	0.89	0.33	------

Material: Nine specimens were collected from bottom samples; two of these (both males) were dissected.

Occurrence: *Philomedes lomae* seemed to be uniformly distributed in the Bimini area (Fig. 38). Specimens were collected in waters having salinities of 36 to 42 parts per thousand, and temperatures of about 29°C. The species was obtained at water depths ranging from one to 20 meters. The bottom in the collecting area was calcareous sand.

Philomedes paucichelata Kornicker, new species

(Figs. 46, 4A–B; 54, A–E; 55, A–C; 87, B, E, H.)

Diagnosis: The shell is elongate, with a prominent rostrum and a posteroventral projection, and is not strongly calcified. The surface is coarsely punctate and contains irregular horizontal ripples as well as light depressions above the central part of the shell.

The fifth leg terminates in a large quadrate tooth. The furca bears six claws; the first, second, and fourth claws are strong; the third, fifth, and sixth claws are weak. Natatory bristles on the second antenna are spined. The seventh leg bears four terminal and two lateral setae. The living ostracode has a characteristic orange-colored body and eyes. The male is unknown.

Comparisons: This species may be distinguished from *Philomedes flexilia* Brady and *Philomedes sculpta* Brady by the fewer number of claws on the furca. The shape of the shell is remarkably similar to that of *Streptoleberis crenulata* Brady but, as the appendage structure of the latter species is unknown, the relationship of these two forms remains in doubt.

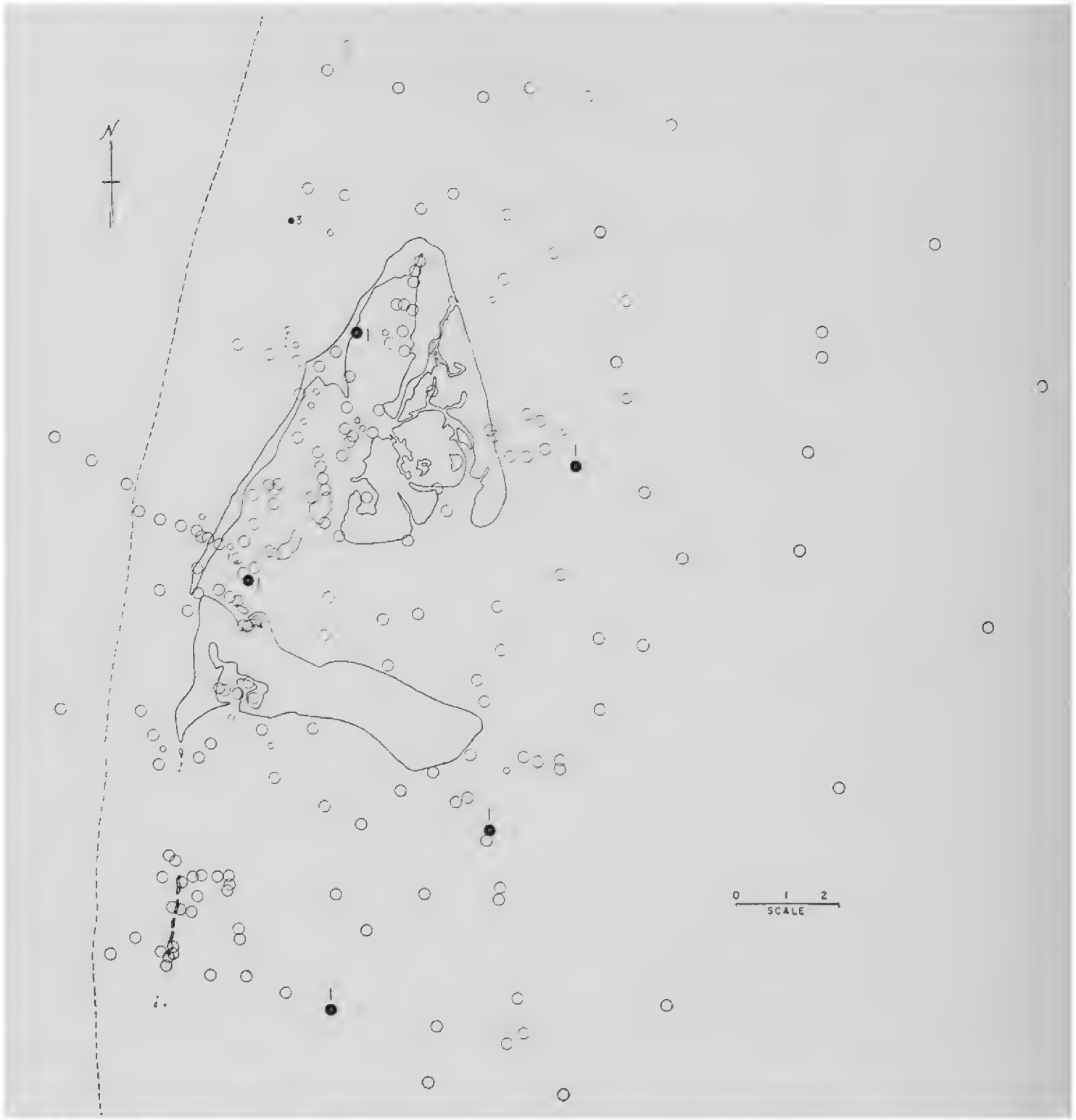

FIG. 38. Distribution of *Philomedes lomae* Juday. Species was absent from samples shown as empty circles. Small circles represent trawl samples; large circles represent spot samples.

Shell measurements (in mm.) :

Specimen number	Length	Width	Height
287–1 (holotype)	0.83	0.35	0.46
62*	0.8	------	0.48
288	0.87	0.35	0.50
156–5	0.80	.....	0.4

* Gravid female.

Material: Eighty-one specimens were collected from bottom samples; two of these (both female) were dissected, and, in addition, individual appendages were examined from several other specimens. The holotype is specimen number 287–1, illustrated on Fig. 46, 4a–b.

Occurrence: *Philomedes paucichelata* was a common species in the Bimini area (Fig.

39). It was found in water from one to about 20 meters in depth. Specimens were collected in waters having temperatures of about 29°C. and salinities of approximately 38 parts per thousand. The bottom in the collecting areas was calcareous sand.

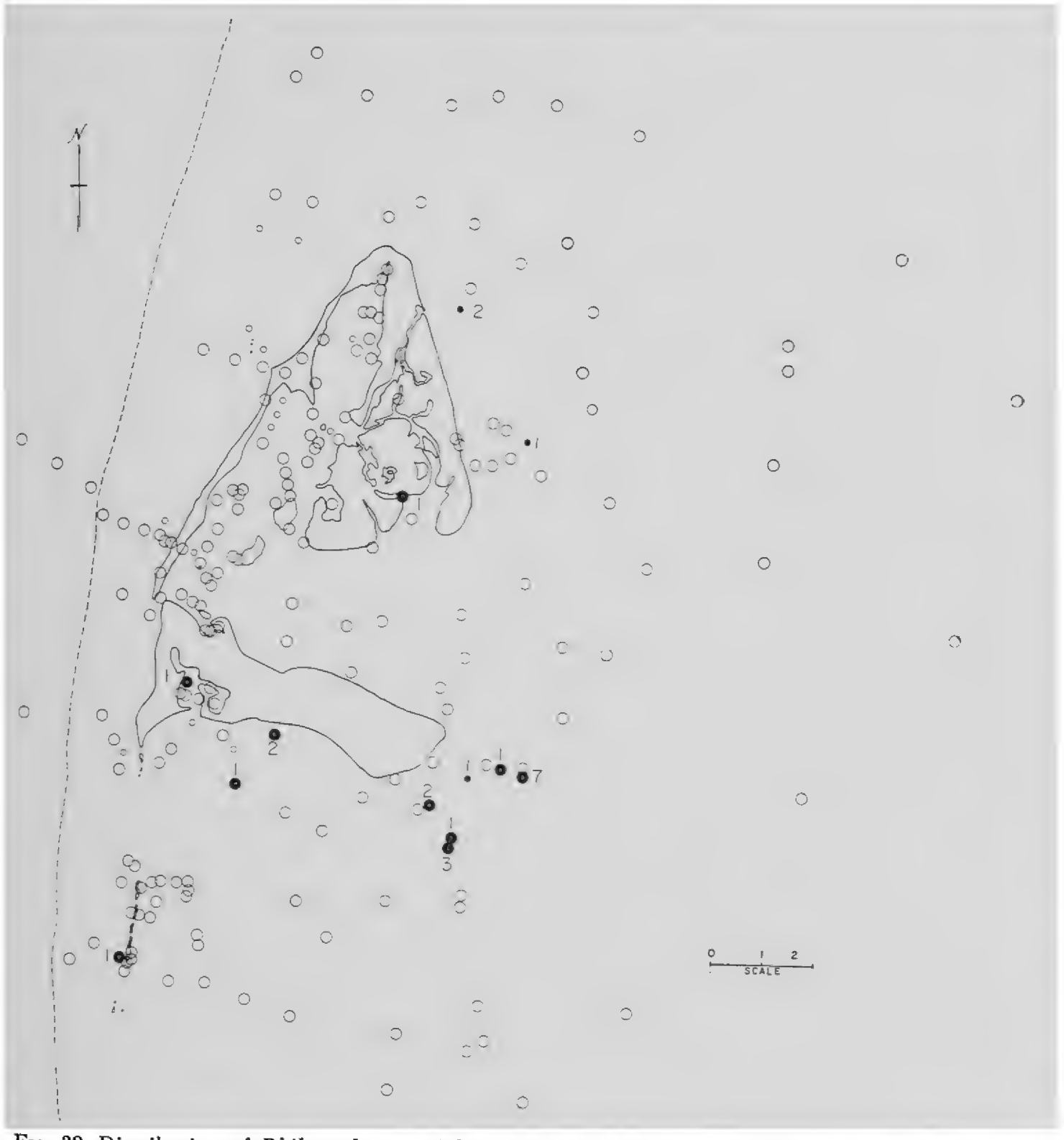

FIG. 39. Distribution of *Philomedes paucichelata* Kornicker, new species. Species was absent from samples shown as empty circles. Small circles represent trawl samples; large circles represent spot samples.

Genus *Pseudophilomedes* Mueller

This genus is characterized by having an elongate tooth on the fifth limb.

Pseudophilomedes ferulana Kornicker, new species

(Figs. 46, 1A–B, 2A–B; 56, A–D)

Diagnosis: The carapace of this species is elliptical in lateral view, with a small rostrum in the upper part of the anterior margin and a short postero-ventral projection.

The caudal furca contains a total of eight claws. The claw arrangement is typical of

the genus: two large claws on the distal end, followed by several smaller claws; the fourth claw is larger than the third, fifth, sixth, seventh, and eighth claws.

The maxilla bears on its end a blunt, elongate process. The remaining appendages are typical of the genus. The seventh limb contains six terminal and four lateral setae. The male is unknown.

Comparisons: Three species of this genus have been described previously: *Pseudophilomedes foveolata* G. W. Mueller; *Pseudophilomedes inflata* (Brady and Norman); and *Pseudophilomedes angulata* Mueller. *P. ferulana* may be distinguished from these forms by having eight furcal claws, whereas *P. foveolata* and *P. angulata* have only six and *P. inflata* has 10.

P. ferulana is also distinguished from the other species in having a long blunt process on the last joint of the maxilla. This feature may be of subgeneric value.

Shell measurements (in mm.):

Specimen number	Length	Width	Height
165–1 (holotype)	1.15	------	0.79
93–1	0.63	------	0.40
118B–3	?0.98	------	------

Material: Five specimens were collected from bottom samples; two of these (both females) were dissected. The holotype is specimen number 165–1, illustrated on Fig. 46, 2a–b.

Occurrence: Three specimens were obtained east of South Bimini, and one west of Turtle Rocks (Fig. 37). Water temperature in collecting area was about 29°C., and the salinity 37 parts per thousand. Water depth was about six meters.

Family Rutidermatidae

Genus *Rutiderma* Brady and Norman

This genus is characterized by having a strong chela on the mandible.

Subgenus *Rutiderma* Kornicker, new subgenus

Diagnosis: Caudal laminae have few (six) claws, which include three or four strong claws followed by two or three weak "claws" with hairs at their base.

Comparisons: Three species, *Rutiderma compressa* Brady and Norman, *Rutiderma rostrata* Juday, and *Rutiderma dinochelata* Kornicker, new species, form the subgenus *Rutiderma* which is based on the furca having few claws which decrease in length posteriorly. The subgenus *Alternochelata* is based on the included species (one at present) having a furca bearing numerous claws, with the strong claws alternating with weak claws and spines.

Rutiderma (Rutiderma) dinochelata Kornicker, new species

Figs. 46, 8A–B; 57, A–F; 58, A–D; 86, B, F, J)

Diagnosis: The shell is oval in lateral view with a truncate posterior. A shallow antennal sinus does not have an overhanging rostrum. The shell surface is coarsely punctate and ornamented with numerous riblets; two prominent longitudinal ribs run almost the complete length of the shell.

The caudal furca bears three strong claws which show distinct demarcation lines at

their bases, followed by two weak claws. The remaining appendages are typical of the genus. The seventh limb bears six terminal and four lateral setae. The male is unknown.

Comparisons: *Rutiderma dinochelata* differs from *Rutiderma compressa* Brady and Norman in the distribution of the strong and weak claws on the furca. *R. dinochelata* differs from *R. rostrata* Juday in not having an overhanging rostrum.

Shell measurements (in mm.):

Specimen number	Length	Width	Height
57–1 (holotype)	1.22	0.45	0.87
91–1	1.18	0.45	0.8
247–10	1.14	-----	0.79

Material: Seventy-nine specimens were collected from bottom samples. Two specimens were dissected (both females), and individual appendages were examined from several additional specimens. The holotype is specimen number 57–1, illustrated on Fig. 46, 8a-b.

Occurrence: *Rutiderma dinochelata* was common in the Bimini area (Fig. 40). Specimens were obtained from waters which ranged in depth from one to 20 meters, and in salinity from 31 to 42 parts per thousand. Water temperature was about 29°C.

Alternochelata Kornicker, new subgenus

Type species: *Rutiderma (Alternochelata) polychelata* Kornicker, new species

Diagnosis: Caudal laminae with many claws; weak claws and spines alternate with strong claws.

Comparisons: The subgenus *Alternochelata* differs from the subgenus *Rutiderma* in having more claws on the furcal laminae and in having these claws arranged so that weak claws and spines alternate with strong claws.

Rutiderma (Alternochelata) polychelata Kornicker, new species
(Figs. 46, 6A–B; 59, A–E; 86, C, G)

Diagnosis: The shell is oval in lateral view, with a narrow antennal sinus and overhanging beak. The postero-ventral corner is compressed, forming a small but distinct projection. The surface of the shell is smooth and without ribs or other ornamentation.

The furca bears 10 claws and spines; two long distal claws are followed by a small annulated spine; then a short claw is followed by a weak claw, which is succeeded by a larger claw and four weak claws. The second antenna bears a secondary appendage which seems to have two joints. The proximal joint of the secondary appendage bears several short spines (five or six), whereas the distal joint bears a long spine which has secondary setae near its middle. The seventh limb contains six terminal and four lateral setae. The first and second antenna, maxilla, and the fifth and sixth limbs are typical of the genus.

Comparisons: *Rutiderma (Alternochelata) polychelata* differs from all previously described species of this genus in possessing a greater total number of claws (10) on the furca and also in that these claws are arranged so that strong and weak claws alternate.

Occurrence: Two specimens were collected east of South Bimini and eight were obtained in North Bimini harbor (Fig. 37). Water depth in collecting areas ranged from

FIG. 40. Distribution of *Rutiderma dinochelata* Kornicker, new species. Species was absent from samples shown as empty circles. Small circles represent trawl samples; large circles represent spot samples.

one to five meters. Temperatures were about 29° C., and salinities were about 37 parts per thousand. The bottom consisted of calcareous sand.

Shell measurements (in mm.):

Specimen number	Length	Width	Height
144–1	1.03	0.49	0.73
110F–2 (holotype)	1.36	0.55	0.98

Material: Ten specimens were collected from bottom samples; one specimen (sex not known) was dissected. The furca of a second specimen was examined and found identical to that of first specimen. The holotype is specimen number 110F–2, illustrated on Figure 86, C, G.

Family Asteropidae

Genus *Asteropina* Strand

Asteropina mulleri (Skogsberg)

(Figs. 60, A-F; 61, A-F; 87, A, D, G)

Cylindroleberis teres G. W. Mueller, 1894, Fauna Neapel, Monogr. Vol. 21, P. 220, Pl. IV, Figs. 13, 30, 43; Pl. V, Figs. 15, 24, 25; Pl. VIII, Fig. 5.

Asterope mulleri Skogsberg, 1920, Uppsala Universitat, Zool. Bidr. Uppsala, Suppl. Ed. 1, PP. 483–491, Fig. LXXXIX; Klie, 1940, Kieler Meeresforshungen, Band 3, PP. 409–411, Figs. 7–10.

Diagnosis: The shell is more or less pear shaped, with its greatest height and width behind the middle, but elliptical shells are occasionally encountered with the greatest height and width in the middle. Live shells have characteristic brown markings on the inner surface of the shell which are visible from the outside. These markings fade after death.

Shell measurements (in mm.):

Specimen number	Length	Width	Height
CP5–1*	1.26	0.49	0.90
CP5–3	1.3	.....	0.87
CP5–2*	1.26	0.57	0.89
CPAC–1	1.34	.....	0.93

* Gravid female.

Remarks: This species is described in considerable detail by Skogsberg (1920). Skogsberg (1920) and Mueller (1894) describe this species as having six claws on the furca. The adults examined by the author (five females) had either five or six furcal claws. One individual contained six on the left lamina and five on the right. The Bimini specimens are slightly smaller than Skogsberg's or Mueller's forms and much smaller than specimens collected by Klie (1940).

Material: Fifty-three specimens were collected in the Bimini area from bottom samples. Seven specimens were dissected; of these three were gravid females, and the sex of the remainder was not determined.

Occurrence: *Asteropina mulleri* was widely distributed in the Bimini area (Fig. 41). It occurred in waters having salinities ranging from about 31 to 39 parts per thousand and temperatures around 29°C. Individuals belonging to this species were adept at agglutinating debris in order to form burrows in which they resided. Occasionally two individuals occupied the same burrow. Mueller (1894, p. 14) noted burrow formation by other members of this genus.

Distribution: Also reported from the English Channel, the Mediterranean Sea, and the coast of German Southwest Africa.

Asteropina setisparsa Kornicker, new species

(Figs. 46, 9A-B; 62, A-D; 63, A-D; 64, A-E; 86, L-P)

Diagnosis: The carapace is elongate with almost parallel dorsal and ventral edges.

FIG. 41. Distribution of *Asteropina mulleri* (Skogsberg) and *Actinoseta chelisparsa* Kornicker, new species. Species was absent from samples shown as empty circles. Small circles represent trawl samples; large circles represent spot samples.

The postero-ventral corner projects slightly in some individuals; in others the posterior end is evenly rounded. In dorsal view the carapace is slightly wider behind than in front. A narrow slit, the antennal sinus, is present in the lower half of the anterior part of the shell.

The furca contains seven to eight claws. The anterior five claws are sturdier than the last two or three. The seventh limb contains six lateral and six terminal setae. The antero-ventral corner of the sixth limb bears one thick bristle and one or two slender bristles; the ventral edge contains, at most, one bristle and many fine hairs. Two large black eyes are visible through the shell. The male is unknown.

Comparisons: The shell of this species is similar to that of *Asterope mariae* Baird. *A. setisparsa* differs from *A. mariae* in having fewer claws on the furca and in the absence of numerous bristles along the ventral edge of the sixth limb. *A. setisparsa* is also smaller than *A. mariae*.

Shell measurements (in mm.):

Specimen number	Length	Width	Height
48–6	1.45	0.53	0.69
246–3* (holotype)	1.54	.....	0.75
127G	1.5	0.57	0.78
122D–3*	1.52	.....	0.77
141K	1.22	0.47	0.63

* Gravid female.

Material: Thirty-seven specimens were collected from bottom samples. Three specimens (all female) were dissected. The holotype is specimen number 246–3 illustrated on Fig. 86. L-P.

Occurrence: *Asteropina setisparsa* was abundant east of South Bimini and rare in other areas (Fig. 42). East of South Bimini where this species reached its greatest abundance. the depth of water from which this species was collected ranged from one to five meters and had a temperature of about 29°C. Salinity at this locality was about 37.5 parts per thousand. The bottom was calcareous sand and rock. Patches of *Thalassia* and the algae *Laurencia* grew in this area. but *A. setisparsa* was not restricted to them.

Asteropina extrachelata Kornicker, new species

(Figs. 65. A-E; 66. A-E; 87, C, F, I)

Diagnosis: The shell is oval in lateral outline and has a smooth surface; however, small pits may be observed under high magnification. The antennal sinus is a narrow slit just below the center of the anterior edge.

The furca bears five claws followed by four annulated bristles. The penultimate joint of the mandible has a "claw" at about the middle of the anterior edge. Along the ventral edge the sixth limb bears approximately 24 bristles. Two bristles are on the anterior edge. and a total of five bristles are on the antero-ventral corner. Six lateral and six terminal setae are on the seventh limb. Two lateral eyes are present as well as the gill-like organs typical of the genus.

Comparisons: The shell is similar to that of *Asterope abyssicola* Sars. *Asteropina extrachelata* differs from *A. abyssicola* in having fewer setae on the seventh leg. The furca of *A. extrachelata* differs from that of *A. abyssicola*. as well as *Asterope mariae* Baird. in that the last four digits are distinctly annulated bristles. whereas the other two species bear weakly developed claws.

Only one individual of this species was collected. The "claw" on the anterior edge of the penultimate joint of the mandible differentiates this species from all other species of this genus known to the author. For this reason a new species was erected with this minimum of individuals.

Shell measurements (in mm.):

Specimen number	Length	Width	Height
118–1* (holotype)	1.88	.....	1.01

* Gravid female.

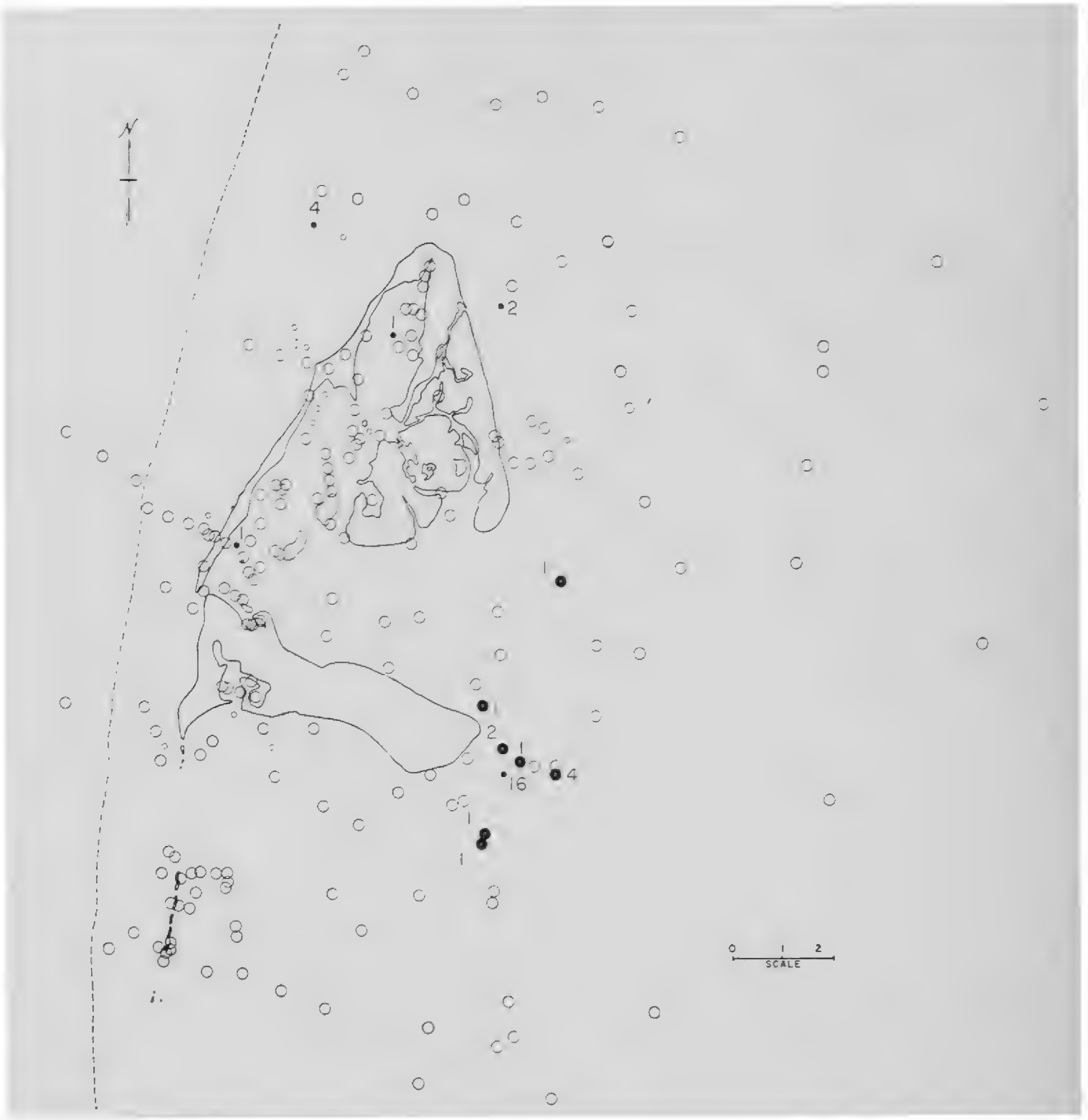

FIG. 42. Distribution of *Asteropina setisparsa* Kornicker, new species. Species absent from samples shown as empty circles. Small circles represent trawl samples; large circles represent spot samples.

Remarks: The individual examined was a female. It contained rosette-like markings on the shell similar to those described by Tressler (1949) on *Cyclasterope sphaerica.* These markings have been observed by the author on some individuals of other species and seem to be due to the decomposition of the soft parts as they are not present on the living animal. A diagram of one of the markings on *A. extrachelata* is presented on Fig. 41, 8c.

Material: One specimen (a female) was collected in a bottom sample. The holotype is specimen number 118–1, illustrated on Fig. 87, C, F, I. Appendages of this specimen are figured on Figs. 65, A-E; and 66, A-E.

Occurrence: The only specimen of *Asteropina extrachelata* collected came from the eastern section of Cavelle Pond, South Bimini. The sediment there gave off an odor of hydrogen sulfide and supported an abundant growth of the algae *Laurencia.*

Genus *Cycloberis* Skogsberg

Cycloberis biminiensis Kornicker, new species

(Figs. 67, A-D; 68, A-F; 85, A-E)

Diagnosis: The shell is oval in lateral outline and only slightly longer than high. An antennal sinus is approximately in the middle of the anterior edge. A distinct muscle scar of rosette form is visible near the center of the shell. Lateral eyes are situated above the muscle scars.

The furca bears four claws followed by three or four bristles. Between the third and fourth claw is an additional small bristle. The seventh limb bears 23 to 32 setae. Six protuberances are on the anterior edge of the penultimate joint of the first antenna. Otherwise, this limb, as well as the frontal organ, is similar to that of *Cycloberis americana* (Mueller). The male is unknown.

Comparison: Many species of *Cycloberis* have a carapace of similar shape. The number and arrangement of claws and bristles on the furca are used for differentiating species. *Cycloberis brevis* (Mueller) is the only species known, other than *C. biminiensis*, whose furca bears four claws; all other known species bear only three claws. *C. biminiensis* differs from *C. brevis* in the presence of a small bristle between the third and fourth furcal claws. *C. brevis* has five to seven bristles following the fourth claw, whereas *C. biminiensis* has only three or four.

Shell measurements (in mm.):

Specimen number	Length	Width	Height
177–1 (holotype)	1.8	0.74	1.4
177–2	1.5	------	1.1
156–1	1.8	0.9	1.3

Material: Seven specimens were collected from bottom samples. Of these specimens three (?females) were dissected, and the caudal furca of two additional specimens examined. The holotype is specimen number 177–1, illustrated on Figs. 85, A-B; 67, A-C, and 68, A-B, D-E.

Occurrence: *Cycloberis biminiensis* was collected in waters ranging in depth from three to 10 meters with temperatures around 20° C. (Fig. 37). The salinity was about 37 parts per thousand.

Actinoseta Kornicker, new genus

Type species: *Actinoseta chelisparsa* Kornicker, new species

Diagnosis: The shell is strongly calcified, densely pitted, and appears imbricate in dorsal view. In the type species the shell is almost oval in lateral view and contains a shallow antennal sinus.

The natatory bristles of the second antenna bear spines on the distal half; basal spines are not present. The posterior appendage of the second antenna bears numerous spines on the first and second joints. The seventh limb has abundant pinnately arranged setae. The furca bears three (always?) sturdy, medium-length claws with fine hairs at the base. Following these claws are a few weak non-annulated setae.

Comparisons: *Actinoseta* is closely related to *Cyclasterope* Skogsberg and *Asterop-*

teron Skogsberg and possesses some of the diagnostic morphological features of both genera. *Actinoseta* differs from *Cyclasterope* in not having powerful basal spines on the second antenna and in having only a few furcal bristles. It differs from *Asteropteron* in having spines on the natatory setae on the second antenna and in possessing numerous setae on the seventh limb.

Actinoseta chelisparsa Kornicker, new genus, new species
(Figs. 46, 10A-B; 43, A-L; 69, A-F; 70, A-I; 89, H-J, P, Q)

Diagnosis: The shell is almost oval in lateral view, with a shallow antennal sinus and small rostrum. The surface of the shell is densely pitted and appears imbricate in dorsal view. Three or four faint protuberances are present in the postero-dorsal corner paralleling the margin. These are not always apparent and are absent on some specimens.

The furca bears three strong claws. At the base of the second and third claws are numerous fine hairs. Occasionally these are also found between the first and second claws. In the posterior corner of the furca are three short, slender bristles. The seventh limb contains about 46 setae which are on about the distal 22 segments; two setae are attached to each segment. The second joint of the posterior appendage of the second antenna bears eight lateral setae. The male is not known. Considerable change in appendage morphology takes place during ontogeny (Fig. 43).

Shell measurements (in mm.):

Specimen number	Length	Width	Height
60–1	1.68	0.92	1.19
CP52–19	0.95	.....	0.73
CP52–16	0.83	.....	0.63
CP52–6*	2.47	.....	1.95
CP38–2* (holotype)	2.42	1.29	1.92
5216B	2.0	.....	1.55
CP52–24	0.61	.....	0.46
CP38–7	0.83	.....	0.71
246–2	0.99	0.55	0.78

* Gravid female.

Material: Thirty-two specimens were collected from bottom samples. Six specimens (all females) were dissected for comparison. Many others were partially dissected during identification. The holotype is specimen number CP38–2, illustrated on Figs. 43, A-L; 69, A-F; 70, B-D, F-I; 89, I, Q.

Occurrence: *Actinoseta chelisparsa* was found in waters three to 15 meters in depth

FIG. 43
Ontogenetic stages in female of *Actinoseta chelisparsa*.

A, D, G, J. Young instar: A, carapace; D, Furca; G, First antenna; J, Posterior appendage of second antenna. Specimen number CP52–16.
B, E, H, K. Immature instar: B, carapace; E, Furca; H, First antenna; K, Posterior appendage of second antenna. Specimen number CP52–19.
C, F, I, L. Mature female: C, carapace; F, Furca; I, First antenna; L, Posterior appendage of second antenna. Specimen number CP38–2.
Figures with similar magnification: A, B, C; D, E, F; G, H, I; J, K, L.

A
B
C
D
E
F
G
H
I
J
K
L

(Fig. 41). Salinity was about 37 parts per thousand and temperature about 29°C. This species was common in Cavelle Pond where salinities as low as 31.5 parts per thousand were recorded.

Genus *Asteropteron* Skogsberg

Asteropteron monambon Kornicker, new species

(Figs. 46, 11A-B; 71, A-G; 72, A-D; 86, D, H, K)

Diagnosis: The shell is elliptical in lateral view, with a shallow antennal sinus slightly below the middle of the ventral margin. The width of the shell increases gradually from the anterior margin to a point about one-fourth of the shell length from the posterior margin and then decreases rapidly so that in dorsal view the carapace resembles the head of an arrow. A raised border parallels the shell's outer edge except at the postero-dorsal corner, where the border forms two or three nodes. These are more distinct on some individuals than on others. A more or less horizontal slightly raised ridge extends from the anterior border, at a point directly behind the antennal sinus, to the posterior portion of the carapace, dying out before reaching the posterior border. In the center of the shell this ridge expands and encloses about 15 reticulations. The surface of the shell is punctate.

The furca is elongate and bears three main claws followed by four smaller secondary claws. The second antenna does not contain basal spines. Natatory bristles of the second antenna also lack spines. The ultimate joint of the secondary branch of the second antenna is covered with fine hairs. The seventh limb bears 16 setae. The terminal part of the seventh limb resembles the "aristotle lantern" of an echinoid. Lateral eyes are not readily visible through the shell. The male is unknown.

Comparisons: *A. monambon* is closely related to *Asteropteron agassizi* (Fr. Mueller) and *Asteropteron fusca* (G. W. Mueller). It is readily distinguished from these two species by the character of the carapace sculpture; *viz.*, the border of *A. monambon* is continuous, and a horizontal ridge approximately bisects the carapace, whereas, the border of *A. agassizi* is discontinuous, and the horizontal ridge runs below the center. The border of *A. fusca* is also discontinuous.

Shell measurements (in mm.):

Specimen number	Length	Width	Height
113G (holotype)	1.25	0.63	0.90
243–1	1.14	0.58	0.83
CP38–1	0.93	.....	0.67
CP52–4	1.52	.....	1.04
91	0.66	.....	0.5
119C	0.61	.....	0.48

Material: Thirty-four specimens were collected from bottom samples. Three specimens (? females) were dissected. The holotype, specimen number 113G, is illustrated on Fig. 46, 11a-b.

Occurrence: *Asteropteron monambon* was fairly uniformly distributed in the Bimini area (Fig. 44). Specimens were collected in waters ranging in salinity from 31.5 to 42 parts per thousand, and in depth from three to about 20 meters. Temperature was about 29°C.

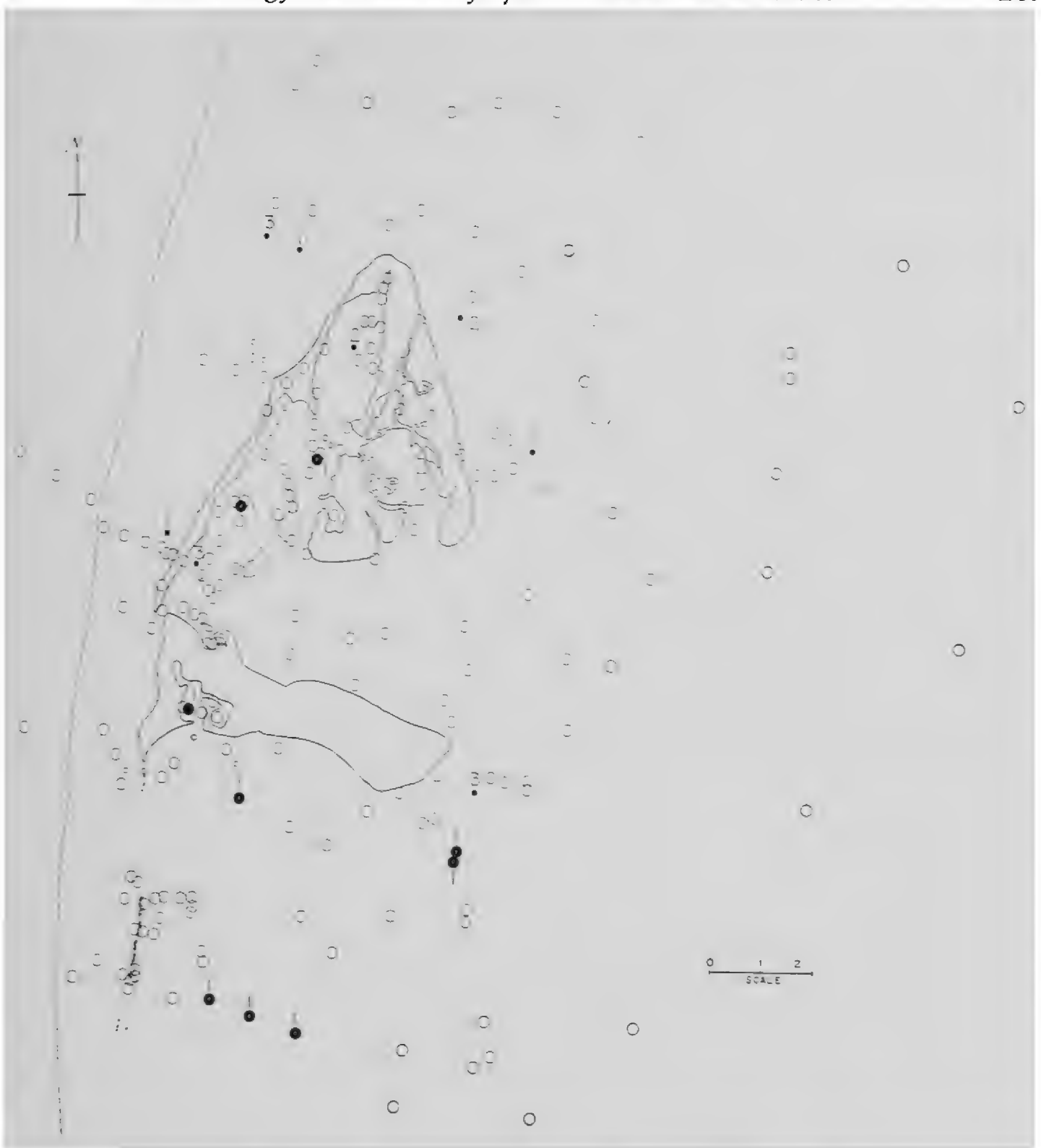

FIG. 44. Distribution of *Asteropteron monambon* Kornicker, new species. Species was absent from samples shown as empty circles. Small circles represent trawl samples; large circles represent spot samples.

Family Sarsiellidae

Genus *Sarsiella* Norman

Sarsiella carinata A. Scott

(Figs. 47, 5A-B; 73, A-G; 74, A-F; 75, A-D; 88, J, N, R; 89, E)

Sarsiella carinata A. Scott, 1905. Rep. Ceylon Pearl Fisheries, Suppl. Rep. 22, P. 368, Fig. 1, 1–2; Fig. 2, 40–41.

Diagnosis: The male shell has a prominent rostrum and a shallow sinus. Two longitudal ribs fringed with short hairs terminate in protuberances posteriorly. A series of hair-covered nodes parallels the ventral margin.

The male furca bears five claws, which increase in length distally. The seventh limb of the male has two lateral and four terminal bristles, and the distal end is closed. The first antenna bears a brush-like sensory organ.

The female shell has ornamentation quite similar to that of the male which differs in having no antennal sinus. Shells of mature females contain marginal radial furrows. The female shell varies in shape and would be difficult to differentiate from other sarsiellids were it not for short stiff hairs which always cover the shells of this species and which are easily visible under high magnification. These hairs are abundant along the horizontal riblets which ornament the shell and around the numerous protuberances along the ventral and dorsal portions of the shell. The horizontal riblets occur, especially on immature individuals, as a series of disconnected protuberances.

The female furca bears five claws followed by two short "points." The seventh limb of the female contains six terminal and two lateral spines; the distal end of the seventh limb is open and bears "teeth." An immature female had only two lateral and two terminal setae on the seventh limb and possessed a closed distal end similar to that of the male.

Comparisons: The female of *S. carinata* resembles *Sarsiella globulus* Brady (Brady and Norman, 1896, Fig. 60, 5–7) from which it differs in having numerous surface protuberances which are covered by short stiff hairs and in possessing fewer spines on the seventh limb. *S. carinata* does not resemble the type species of *S. globulus* (Brady, 1881–1886, Fig. 15, 8–9).

Shell measurements (in mm.):

Specimen number	Length	Width	Height	Sex
686–X2	1.42	0.67	1.12	Female
CP38–5	1.28	.....	0.86	Female
CP38–13	1.48	.....	1.14	Female
CP52–23	1.18	.....	0.68	Male

Remarks: Females of this species have not previously been reported.

Material: Seventy-eight specimens were collected from bottom samples. Eight males were among the collected specimens. Three individuals were dissected.

Occurrence: *Sarsiella carinata* was the most abundant species of the genus *Sarsiella* in the Bimini area. It was especially abundant in North Bimini harbor in front of the Lerner Marine Laboratory. Specimens were collected in water ranging in depth from one to 20 meters, and in salinity from 31.5 to about 38 parts per thousand. Temperature was about 29°C. Areal distribution of the family Sarsiellidae is shown in Fig. 45.

Distribution: This species has been reported from near Ceylon (A. Scott, 1905).

Sarsiella capillaris Kornicker, new species
(Figs. 47, 7A-B; 76, A-F and H; 89, A, B, D, F, O)

Diagnosis: The shell is subcircular in side view, with a posterior projection. Numerous protuberances are present on the surface of the shell. A long hair, which is annulated and becomes wider at about two-thirds of the distance from its proximal end, projects from the apex of each protuberance. Surrounding the base of the long hair are many shorter hairs which may have bulbous tips. The posterior projection of the shell bears many long and short hairs similar to those on the protuberances.

The furca bears five claws followed by several "points." The seventh limb contains four terminal and two lateral setae. The balance of the appendages are typical of the genus. The male is not known.

Comparisons: *Sarsiella capillaris* is difficult to differentiate from some individuals of

FIG. 45. Distribution of the family Sarsiellidae. Genus was absent from samples shown as empty circles. Small circles represent trawl samples; large circles represent spot samples.

Sarsiella carinata Scott, and especially from immature forms of that species. The presence of short stiff surface hairs on *S. carinata* permits differentiation from *S. capillaris* whose surface hairs are slightly longer and appear to be more pliable. Examination of surface hairs is best accomplished under high magnification. *S. capillaris* also differs from *S. carinata* in having fewer terminal spines on the seventh limb.

Shell measurements (in mm.):

Specimen number	Length	Width	Height	Sex
92–1 (holotype)	1.15	0.56	1.15	Female
CP38–10	1.1	.....	0.81	Female
CP52–15	0.82	.....	0.66	Female
1117C–3	0.65	.....	0.49	Female

Material: Fifteen specimens were collected from bottom samples. One ostracode was

completely dissected and several others partially dissected. The holotype is specimen number 92–1, illustrated on Fig. 47, 7a-b.

Occurrence: *Sarsiella capillaris* was found in waters ranging in depth from two to 20 meters, and in salinity from 31.5 to about 37.5 parts per thousand.

Sarsiella gigacantha Kornicker, new species
(Figs. 47, 8A-B; 76; 77, A-E; 88, A, F, H, I)

Diagnosis: The carapace is sub-oval in outline, with the posterior truncate. The male has a rostrum and surface riblets. A prominent spine occurs in the postero-dorsal part of the shell of both sexes.

The caudal lamina bears five strong claws followed by several small "points." The seventh limb of the female contains four terminal and 11 lateral setae.

Comparisons: The postero-dorsal spine on the carapace and the numerous spines on the seventh limb distinguishes *S. gigacantha* from previously described ostracodes of the genus *Sarsiella.*

Shell measurements (in mm.) :

Specimen number	Length	Width	Height	Sex
190–1A (holotype)	1.37	0.75	1.14	Female
122D–2	1.3	------	0.85	Male

Material: Forty-seven specimens were collected in bottom samples. Three specimens were males. Two ostracodes were dissected. The holotype is specimen number 190–1A, illustrated in Fig. 47, 8a-b.

Occurrence: *Sarsiella gigacantha* was found in waters ranging in depth from one to 20 meters, and in salinity from 31.5 to about 38 parts per thousand. Temperature was about 29°C.

Sarsiella truncana Kornicker, new species
(Figs. 78, A-E; 88, Q; 89, C)

Diagnosis: The shell is elliptical in lateral view, except for the truncate posterior. A shallow sulcus separates the slightly inflated postero-dorsal part of the carapace from the anterior part. The surface of the shell is covered with short hairs and minute punctae. The furca bears five to seven claws. The seventh limb contains six terminal and four lateral spines. The male is not known.

Comparisons: The shell of *S. truncana* does not resemble any previously described species.

Shell measurements (in mm.) :

Specimen number	Length	Width	Height	Sex
CP52–21 (holotype)	1.3	0.69	1.13	Female*
CP38–5	0.8	------	0.67	Female
CP38–6	0.41	0.18	0.35	Female
246–3	1.36	------	1.3	Female*
121D–5	1.01	------	0.92	Female*

* Gravid.

Material: Fifty-four specimens were collected from botton samples. Two specimens were dissected. The holotype is specimen number CP52–21, illustrated on Fig. 88, Q; 89, C. Appendages from this specimen are figured on Fig. 78, A, B. D.

Occurrence: *Sarsiella truncana* was abundant east of South Bimini and in North Bimini harbor. Specimens were found in waters ranging in depth from one to 20 meters, and in salinity from 31.5 to about 38 parts per thousand. Temperature was about 29°C.

Sarsiella punctata Kornicker, new species
(Figs. 47, 3A-B; 79, A-I; 88, L, P, M)

Diagnosis: The shell is sub-oval, with posterior truncated. A shallow sulcus extends from the center of the dorsal edge almost to the posterior margin. The surface of the shell is distinctly punctate and without hairs. The furca bears five claws. The seventh limb of the female contains six terminal and four lateral setae. The male has a slight rostrum and two faint horizontal riblets in the posterior part of the shell.

Comparisons: *Sarsiella punctata* differs from *Sarsiella truncana* Kornicker in the absence of surface hairs and in having large punctae. *S. punctata* differs from *Sarsiella gracilis* Scott in not having setae or spines combined with claws on the furca. *Sarsiella crispata* Scott differs from *S. punctata* in having only four furcal claws. *S. punctata* differs from *Sarsiella murrayana* T. Scott in having terminal "teeth" and more setae on the seventh limb.

Shell measurements (in mm.):

Specimen number	Length	Width	Height	Sex
82–1 (holotype)	1.1	0.53	0.81	Female
246–6	0.97	------	0.69	Female
119A–1	0.98	0.57	0.77	Male
CP38–4	1.26	------	1.02	Female
CP38–9	1.04	------	1.0	Female

Material: Nineteen specimens were collected from bottom samples. Two males were among the specimens collected. One male and one female were dissected. The holotype is specimen number 82–1, illustrated on Fig. 47, 3a-b.

Occurrence: *Sarsiella punctata* was common in Cavelle Pond and in North Bimini harbor. Specimens were found in waters which ranged in depth from one to five meters, and in salinity from 31.5 to about 38 parts per thousand. The water temperature was about 29°C.

Sarsiella costata Kornicker, new species
(Figs. 47, 4A-B; 80, A-E; 81, A-E; 88, B, C, G)

Diagnosis: The shell is sub-oval in lateral view, with a truncated posterior. The surface of the shell is punctate. Surface ribs diverge from the postero-dorsal corner of the carapace and meet ventrally. A horizontal, anteriorly directed riblet branches from the lower rib in the postero-ventral quarter of the carapace. The male has a prominent rostrum and surface rib distribution similar to that of the female.

The furca bears five claws followed by two "points." The seventh leg of the mature female contains six terminal and four lateral setae.

Comparisons: The surface rib pattern differentiates *Sarsiella costata* from previously described species of the genus *Sarsiella.*

Shell measurements (in mm.):

Specimen number	Length	Width	Height	Sex
156–2 (holotype)	1.02	0.58	0.79	Female
CP52–7	0.97	.....	0.61	Male
CP38–8	0.73	0.26	0.47	Female
CP38–16	1.14	.....	0.84	Female

Material: Forty specimens were collected from bottom samples. Only one male was among those collected. Three specimens were dissected. The holotype is specimen number 156–2 and is illustrated in Fig. 88, C, G and Fig. 47, 4a-b.

Occurrence: *Sarsiella costata* was especially abundant east of South Bimini. Many specimens were also found in Cavelle Pond. The depth of water from which this species was collected ranged from one to five meters, with a salinity ranging from 31.6 to I2 parts per thousand. Temperature was about 29°C.

Sarsiella sculpta Brady

(Figs. 47, 6A-B; 82, D, E; 88, D, K, E, O, S)

Sarsiella sculpta Brady, 1890, Trans. Roy. Soc. Edinb., Vol. 35, P. 516, Pl. 1, Figs. 17–20; 1897, Brady, Trans. Zool. Soc. Lond., Vol. 13, P. 93.

Diagnosis: The shell is oval in side view, with a small retral process. The postero-dorsal quarter is globose. Two surface riblets diverge posteriorly; one riblet bisects the globose postero-dorsal quarter. The shell surface is coarsely punctate. Mature individuals have radial riblets along the shell margin.

The furca bears five claws followed by several minute "points." The seventh limb contains six terminal and seven lateral setae. The remaining appendages are typical of the genus.

Comparisons: Brady (1890) in the original description of *Sarsiella sculpta* illustrates two individuals differing considerably in appearance. It is questionable as to whether both individuals belong to the same species. The Bahamian individuals are similar to the first individual illustrated by Brady (Pl. 1, Figs. 17, 18). Brady later (1898) illustrated a caudal furca and the end of a seventh limb obtained from a third specimen of *S. sculpta;* the shell of this specimen was not illustrated. The appendages of the Bahamian forms are similar to those presented by Brady, with the exception of two small spines on the fourth claw of the caudal furca which are not present on the Bahamian specimen examined.

Shell measurements (in mm.):

Specimen number	Length	Width	Height	Sex
127–1	1.65	.....	1.45	Female
177	1.54	.....	1.31	Female*

* Gravid.

Material: Thirteen specimens (females) were collected in bottom samples. One specimen was dissected.

Occurrence: *Sarsiella sculpta* was collected in waters which ranged in depth from two to 20 meters. Salinity was about 37.5 parts per thousand and temperature was about 29°C.

Distribution: This species has been collected from Numea (dredged in two to four fathoms), Levuka (from between tidemarks), Vuna Point (from between tidemarks), and Flinders Passage (taken in seven fathoms).

Chelicopia Kornicker, new genus

Type species: *Chelicopia arostrata* Kornicker, new species

Diagnosis: The shell of the male and female are sub-oval (the male is slightly more elongate than the female). The male and female are without rostrum or sinus. The carapace of the type species is covered by hair.

The furca contains many short and long claws. The first antenna is five-jointed. The secondary appendage of the female second antenna is three-jointed, with spines on each joint. The secondary appendage of the male second antenna is two-jointed, with spines on each joint. The ultimate joint is annulated. Other appendages are similar to those of the genus *Sarsiella*.

Comparisons: *Chelicopia* differs from the genus *Sarsiella* in having small claws between the large claws on the furca and in the absence of a rostrum on the male shell.

Chelicopia arostrata Kornicker, new genus, new species

(Figs. 47, 2A-B; 82, A-C; 83, A-D; 84, A-E; 89, G, K-N)

Diagnosis: The shell is sub-oval in lateral view and covered with short hairs. The male is without sinus or rostrum and is slightly longer than the female. Distinct lineated pores parallel the shell margin on the inside.

The first, second, and fourth furcal claws are larger and do not have a line of demarcation at the base. The third and remaining four smaller claws have lines of demarcation at their bases. The secondary appendage of the second antenna of the female is three-jointed (joining indistinct) and has two or three bristles on each joint. The secondary appendage of the male is two-jointed, with the second joint annulated; two bristles are on each joint. The seventh limb contains four terminal and two lateral setae. The rema'ning appendages are similar to those of the genus *Sarsiella*.

Shell measurements (in mm.):

Specimen number	Length	Width	Height	Sex
91–1 (holotype)	1.06	0.66	0.96	?Female
CP38–16	0.78	.....	0.76	?Female
118A–1	0.98	0.51	0.82	Male

Material: Five specimens were collected from bottom samples. Three specimens (two females and one male) were dissected. The holotype is specimen number 91–1, illustrated on Fig. 47, 2a-b.

Occurrence: *Chelicopia arostrata* was found in Cavelle Pond and North Bimini harbor. The waters in which specimens were collected had a salinity range of about 31.5 to 39 parts per thousand. The depth was from one to three meters, and the temperature about 29°C.

Summary and Conclusions

This paper describes a study of the relationship of living and dead ostracodes to the substrate, salinity and other factors in the diverse environments around Bimini.

1. Evidence was found indicating that substrate, salinity, and current velocity affected distribution of ostracodes. Dissolved oxygen, pH, water color, organic detritus, organic content of the sediment, water depth, and daily temperature variation had little effect in the Bimini area. Several species of Myodocopa were found to be positively responsive to light.

2. Living Myodocopa were abundant, but empty carapaces were not found in the sediment possibly because of the low calcium carbonate content of the carpaces of individuals in this suborder. Common species belonging to the suborders Podocopa and Platycopa found as empty carapaces in the sediment were also collected alive in the Bimini vicinity except in the North Sound and Cavelle Pond areas where certain podocopid species occurred commonly as empty carapaces but were not found alive.

3. Brackish water ostracode remains were abundant in the sediment of Cavelle Pond, but only normal marine forms were collected alive in the pond. This is interpreted as indicating that the pond had previously contained brackish water. This interpretation is supported by the fact that a pass connecting Cavelle Pond to the sea is of recent origin.

The occurrence of the relict faunal remains in the sediment of Cavelle Pond suggests that the numerous investigations being carried out today in which animal remains are being correlated with existing environments should be supplemented with a study of the living animal distribution.

4. The sediments containing the largest number of dead ostracodes did not occur in areas containing the largest number of living ostracodes. Empty ostracode carapaces were most abundant in areas where the salinity of the water was either high, low, or extremely variable. Lack of dilution by calcareous remains of other organisms is advanced as the reason for high concentration of empty carapaces in these areas.

5. The evidence in the Bimini area indicates that, in general, remains of the suborders Podocopa and Platycopa found in sediment reflect the kinds but not the absolute numbers of ostracodes of these suborders which were living in the area, and that the suborder Myodocopa was probably more widespread in the past than is indicated by its poor representation in the fossil record.

6. Ostracodes were differentiated taxonomically on the basis of appendage morphology as well as shell structure. Appendage morphology is especially important for differentiation of the suborder Myodocopa which was represented in Bimini waters by 10 genera, two of which are new (*Actinoseta* and *Chelicopia*), and 19 species, including 14 new species and one new subspecies.

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Appendix

Diagrams and Photographs of Ostracode Morphology

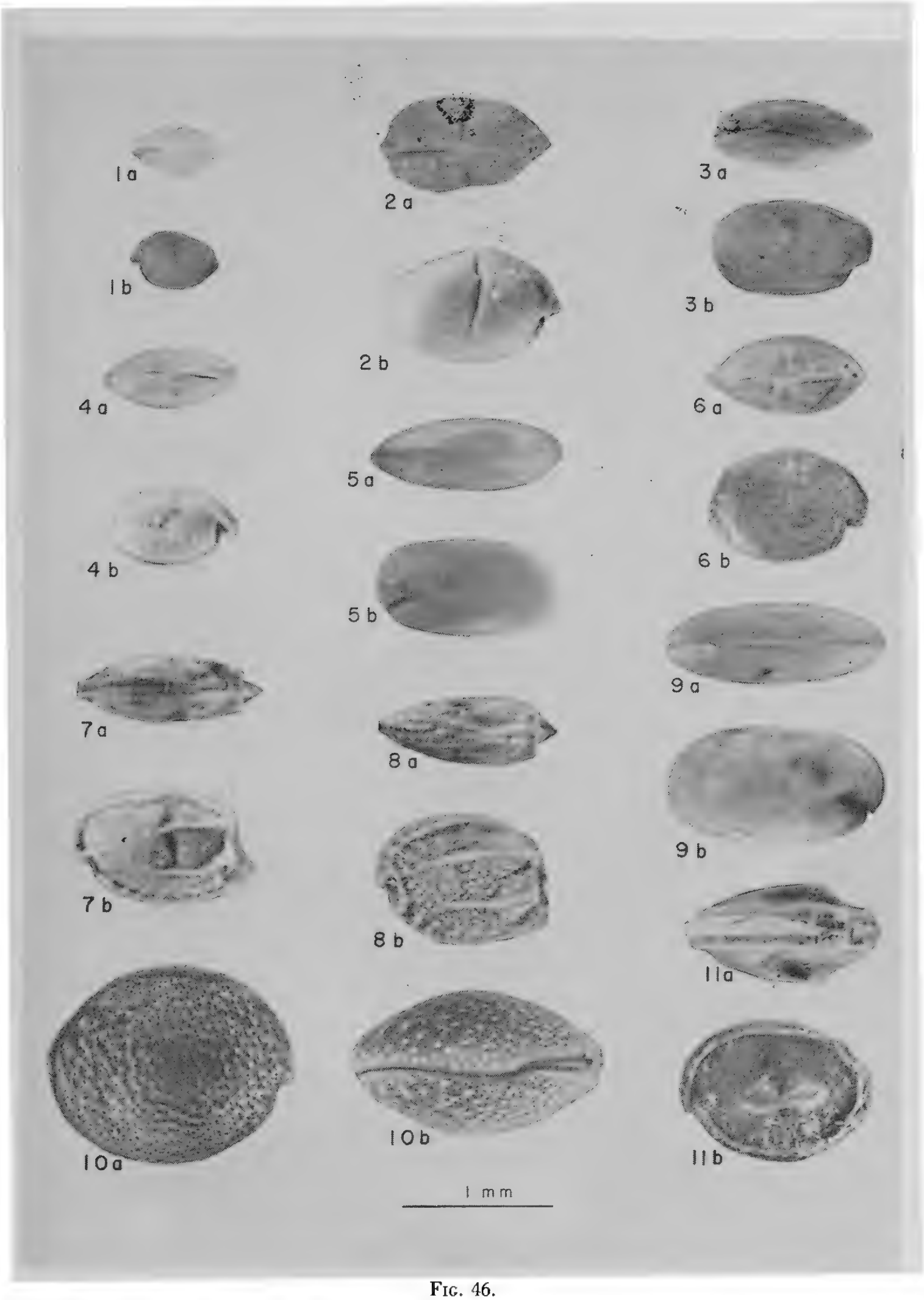

FIG. 46.

1a–b. *Pseudophilomedes ferulana* Kornicker, new species, immature instar. 1a. Dorsal view; 1b. Side view. No. 93–1.
2a–2. *Pseudophilomedes ferulana* Kornicker, new species. 2a. Dorsal view; 2b. Side view. No. 165–1.
3a–b. *Philomedes multichelata* Kornicker, new species. 3a. Dorsal view; 3b. Side view. No. 686Z–6.
4a–b. *Philomedes paucichelata* Kornicker, new species. 4a. Dorsal view; 4b. Side view. No. 287–1.
5a–b. *Asteropina setisparsa* Kornicker, new species. 5a. Dorsal view; 5b. Side view. No. 141K.
6a–b. *Rutiderma polychelata* Kornicker, new species. 6a. Dorsal view; 6b. Side view. No. 144–1.
7a–b. *Philomedes lomae* (Juday). 7a. Dorsal view; 7b. Side view. No. 115–C1.
8a–b. *Rutiderma dinochelata* Kornicker, new species. 8a. Dorsal view; 8b. Side view. No. 57–1.
9a–b. *Asteropina setisparsa* Kornicker, new species. 9a. Dorsal view; 9b. Side view. No. 48–6.
10a–b. *Actinoseta chelisparsa* Kornicker, new species. 10a. Side view; 10b. Dorsal view. No. 60–1.
11a–b. *Asteropteron monambon* Kornicker, new species. 11a. Dorsal view; 11b. Side view. No. 113G.

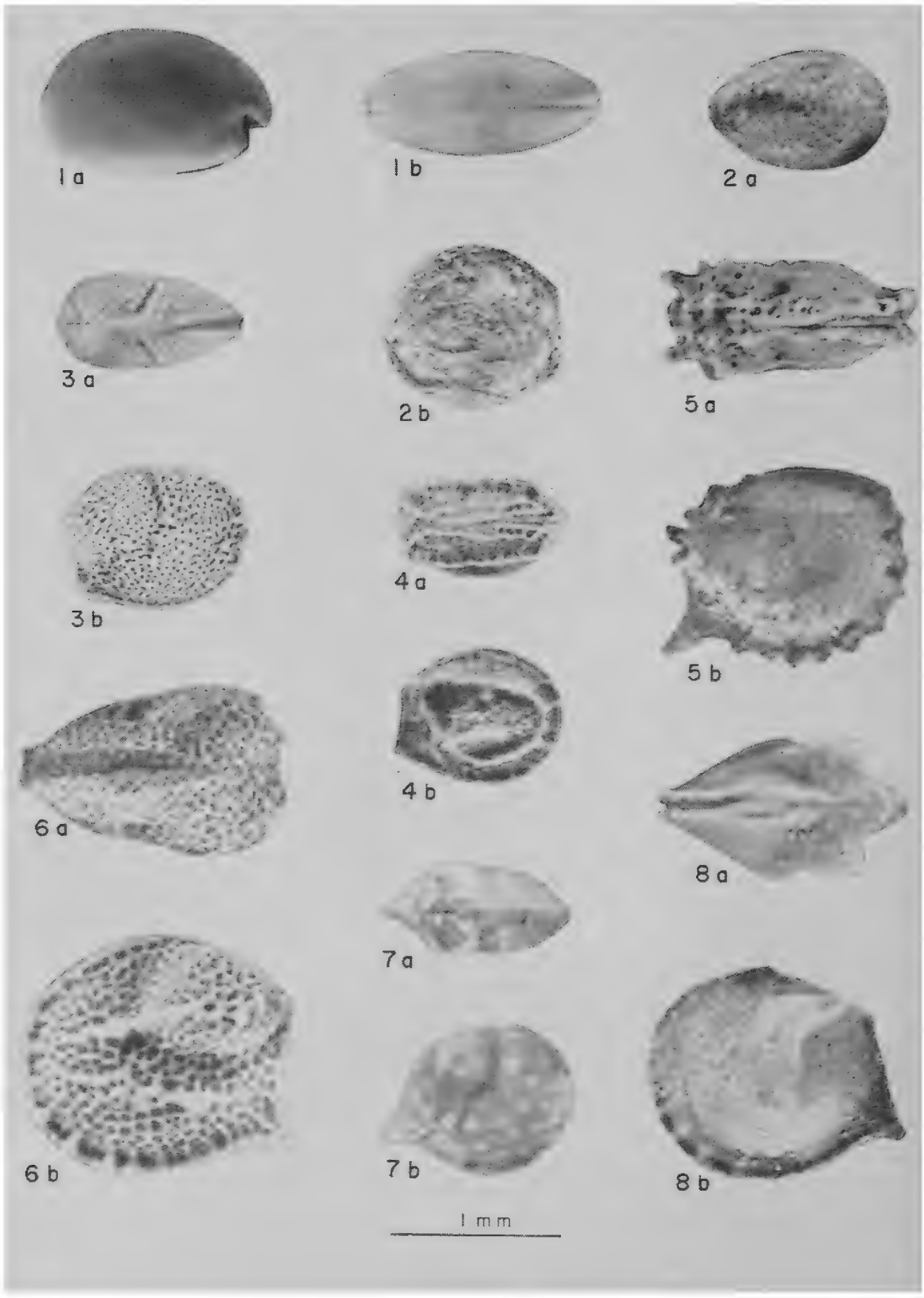

FIG. 47.

1a–b. *Cypridina squamosa lerneri* Kornicker, new subspecies. 1a. Side view; 1b. Dorsal view. No. 212–1.
2a–b. *Chelicopia arostrata* Kornicker, new species. 2a. Dorsal view; 2b. Side view. No. 91–1.
3a–b. *Sarsiella punctata* Kornicker, new species, female. 3a. Dorsal view; 3b. Side view. No. 82–1.
4a–b. *Sarsiella costata* Kornicker, new species, female. 4a. Dorsal view; 4b. Side view. No. 156–2.
5a–b. *Sarsiella carinata* A. Scott, female. 5a. Dorsal view; 5b. Side view. No. 686X–2.
6a–b. *Sarsiella sculpta* Brady, female. 6a. Dorsal view; 6b. Side view. No. 127–1.
7a–b. *Sarsiella capillaris* Kornicker, new species, female. 7a. Dorsal view; 7b. Side view. No. 92–1.
8a–b. *Sarsiella gigacantha* Kornicker, new species, female. 8a. Dorsal view; 8b. Side view. No. 190–1A.

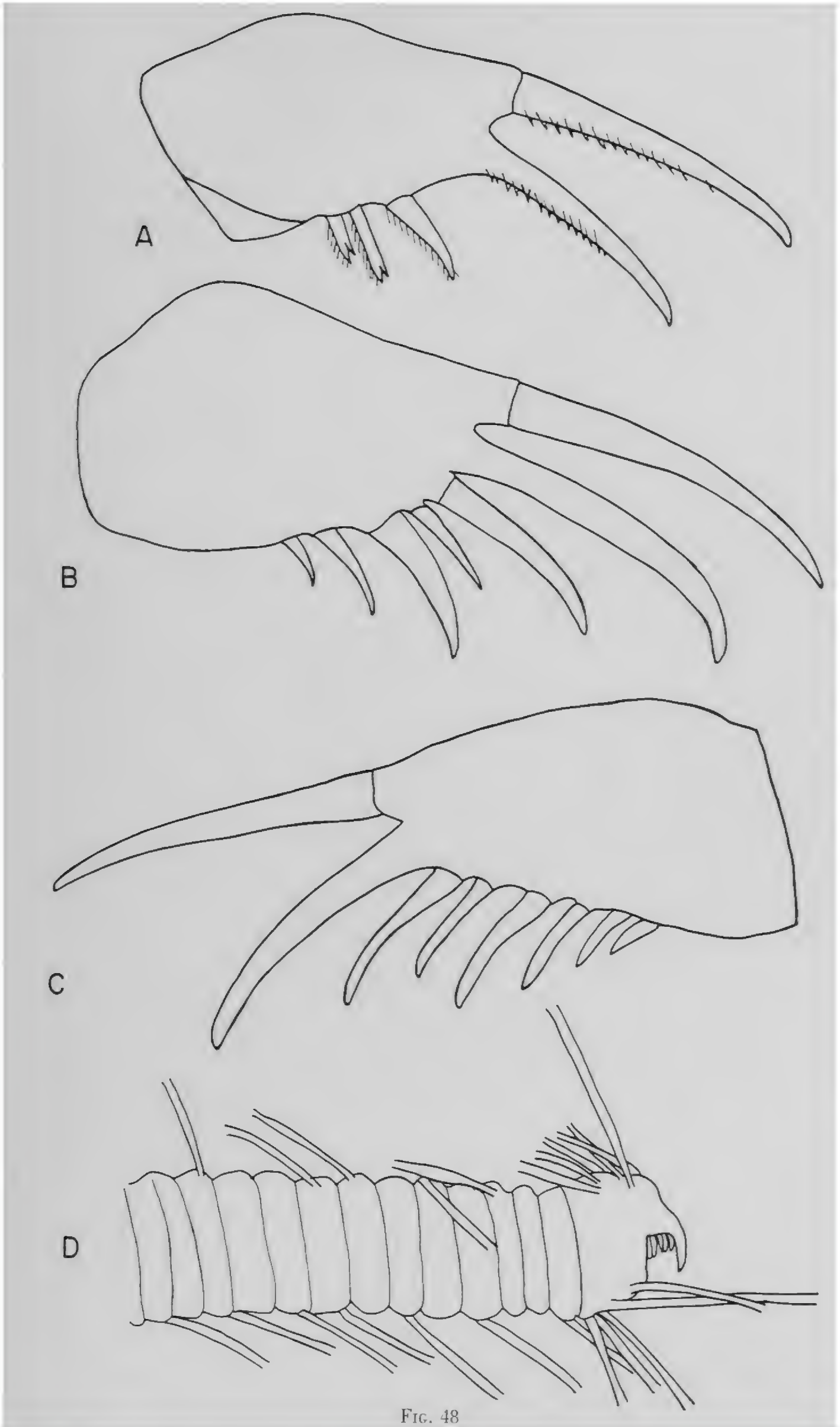

FIG. 48

Cypridina squamosa lerneri Kornicker, new subspecies.

A. Furca. Specimen No. P–1 (juvenile).
B. Furca. Specimen No. 246–7 (juvenile).
C. Furca. Specimen No. 247–3 (gravid female).
D. Seventh limb. Specimen No. 119–1 (mature male).

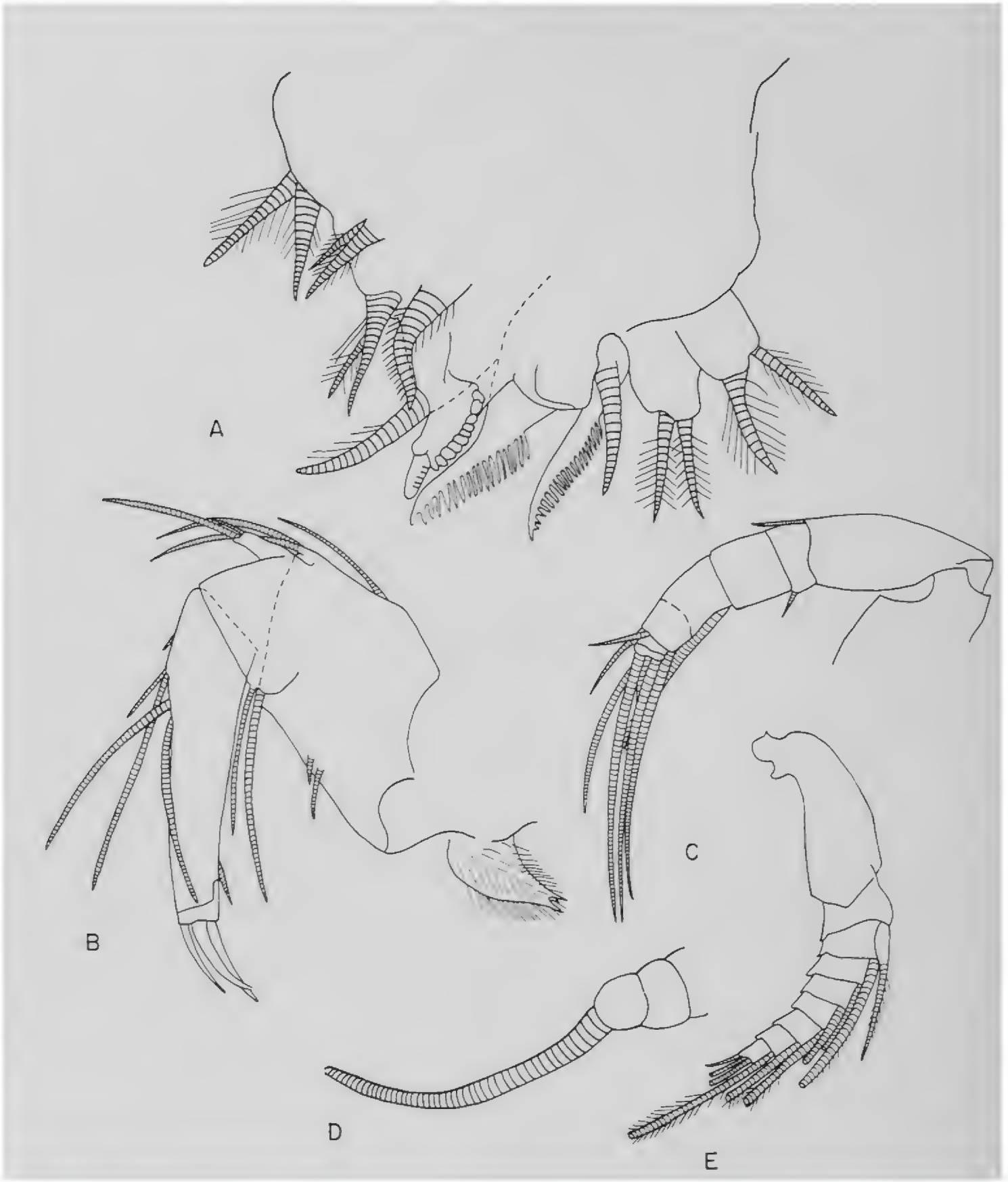

FIG. 49.

Cypridina squamosa lerneri Kornicker, new subspecies.

A. Portion of maxilla or fifth limb of young instar. Specimen No. P–1 (juvenile).

B. Mandible of young instar. Specimen No. P–1 (juvenile).

C. First antenna young instar. Specimen No. P–1 (juvenile).

D. Secondary branch second antenna. Specimen No. P–1 (juvenile).

E. Second antenna. Specimen No. P–1 (juvenile).

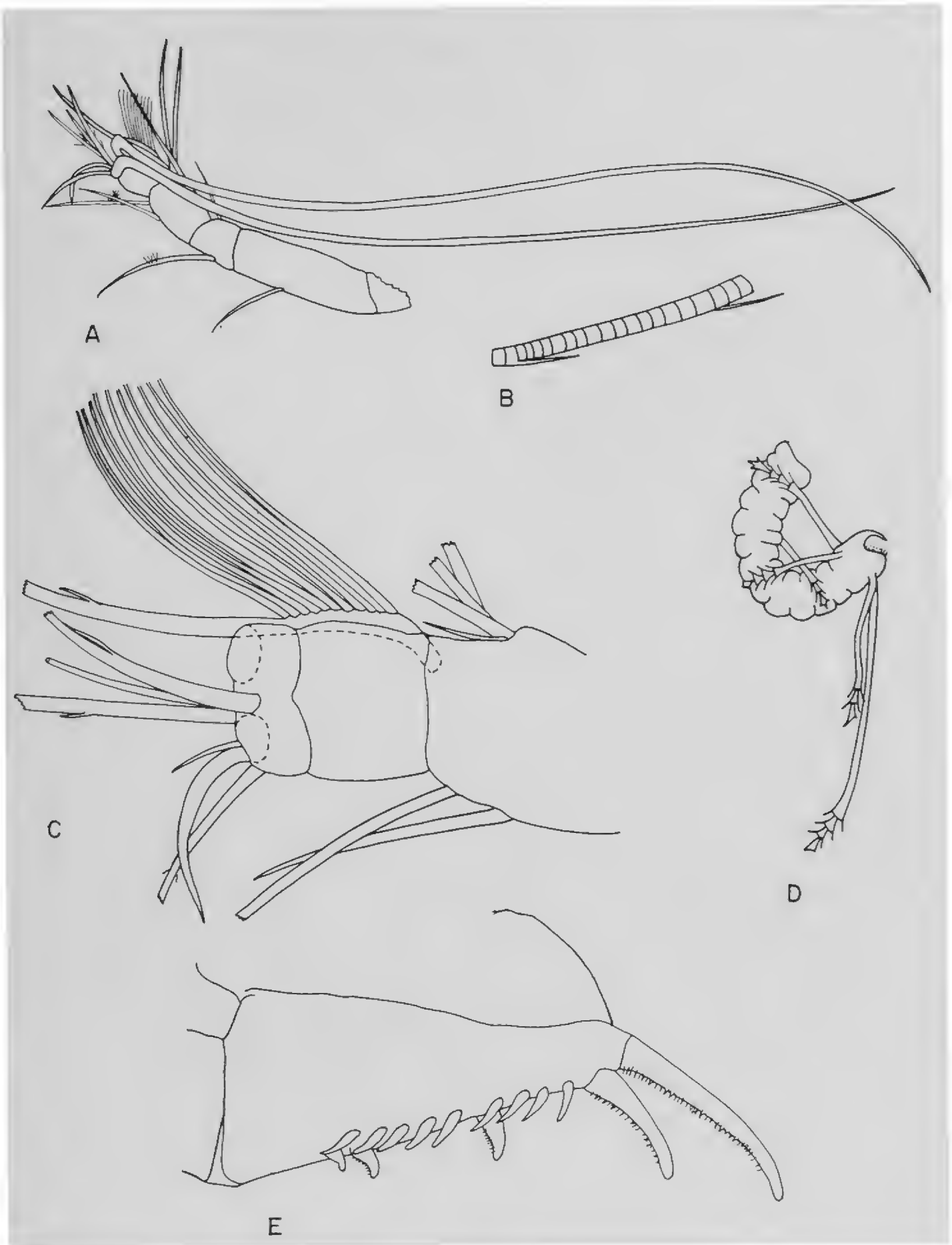

FIG. 50.

Philomedes multichelata Kornicker, new species (Male).

A. First antenna. Specimen No. 686Z–2.

B. Portion of sensory setae of first antenna enlarged. Specimen No. 686Z–2.

C. Distal end first antenna; sensory setae not shown. Specimen No. 686Z–2.

D. Seventh limb. Specimen No. 686Z–3.

E. Furca. Specimen No. 686Z–4.

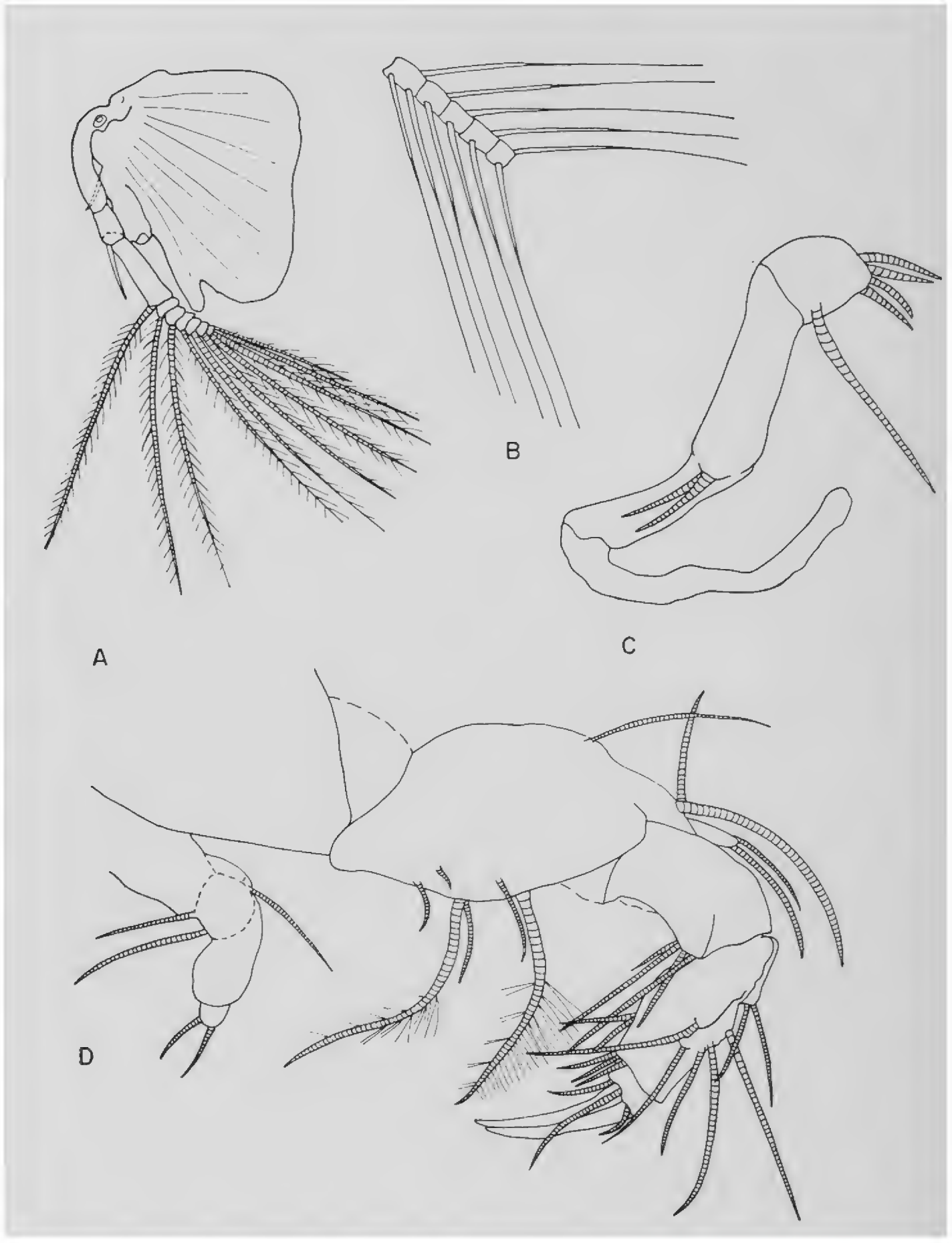

FIG. 51.

Philomedes multichelata Kornicker, new species (Male).

A. Second antenna. Specimen No. 686Z–2.

B. Portion of sensory bristle enlarged. Specimen No. 686Z–2.

C. Secondary branch of second antenna. Specimen No. 686Z–4.

D. Mandible. Specimen No. 686Z–4.

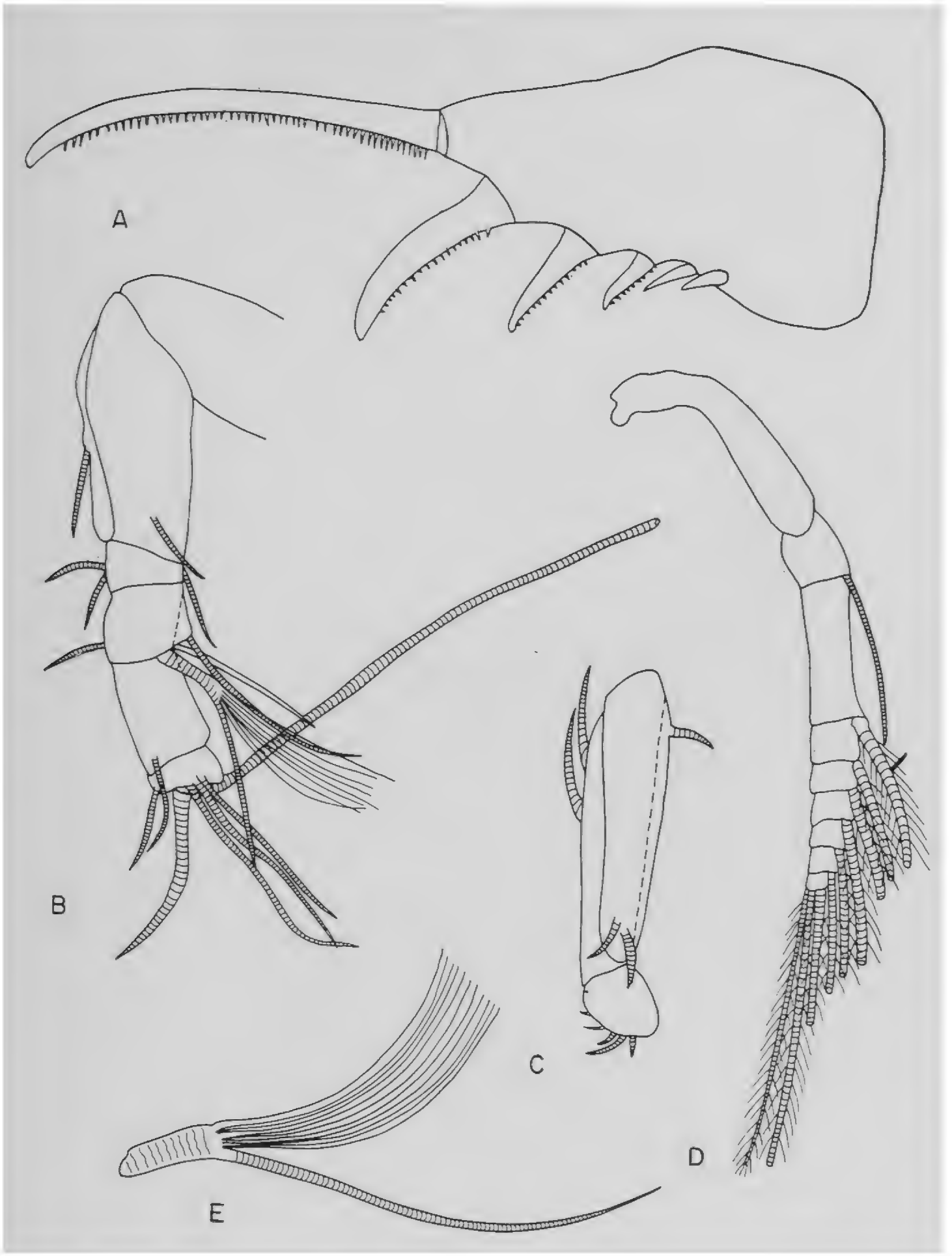

FIG. 52.

Philomedes lomae Juday (Male).

A. Furca. Specimen No. CP52–12.

B. First antenna. Specimen No. CP52–12.

C. Secondary branch of second antenna. Specimen No. CP52–12.

D. Second antenna. Specimen No. CP52–12.

E. Sensory bristle of first antenna. Specimen No. CP52–12.

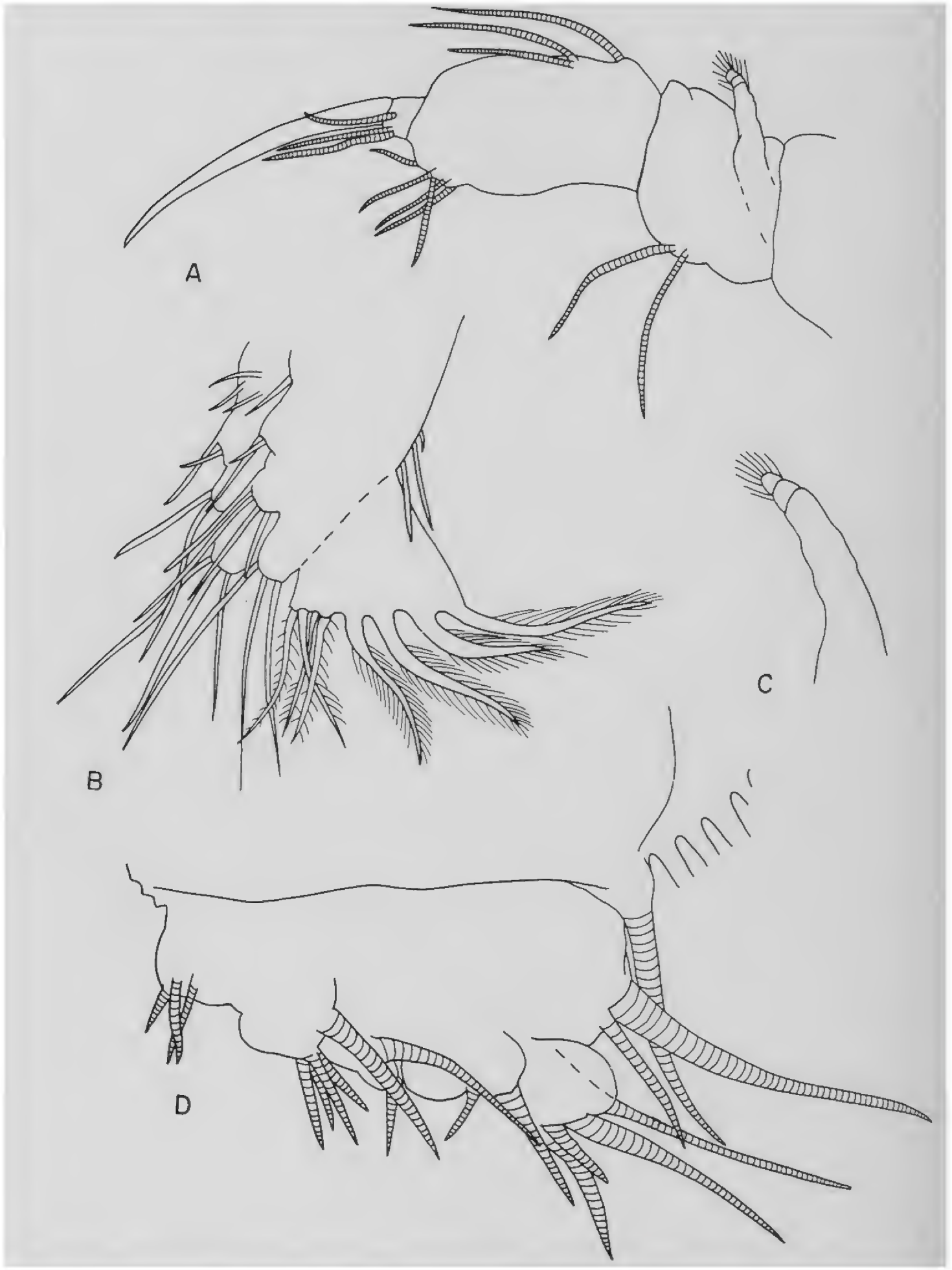

FIG. 53.

Philomedes lomae Juday (Male).

A. Mandible. Specimen No. CP52–12.

B. Portion of sixth limb. Specimen No. CP52–12.

C. Sensory appendage on mandible. Specimen No. CP52–12.

D. Portion of fifth limb. Specimen No. CP52–12.

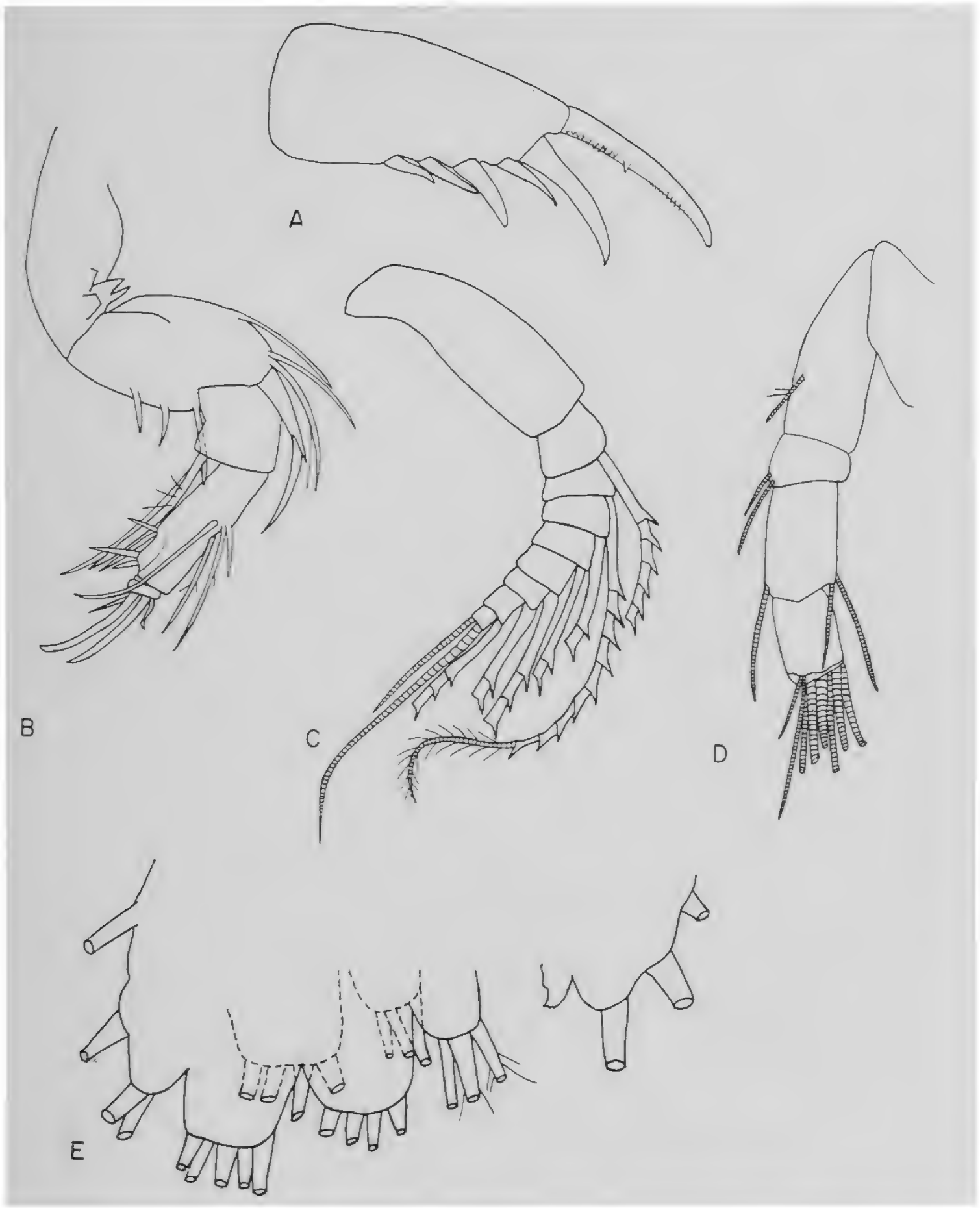

FIG. 54.

Philomedes paucichelata Kornicker, new species (Female).

A. Furca. Specimen No. 156–5.

B. Mandible. Specimen No. 156–5.

C. Second antenna. Specimen No. 156–5.

D. First antenna. Specimen No. 156–5.

E. Part of sixth leg. Specimen No. 156–5.

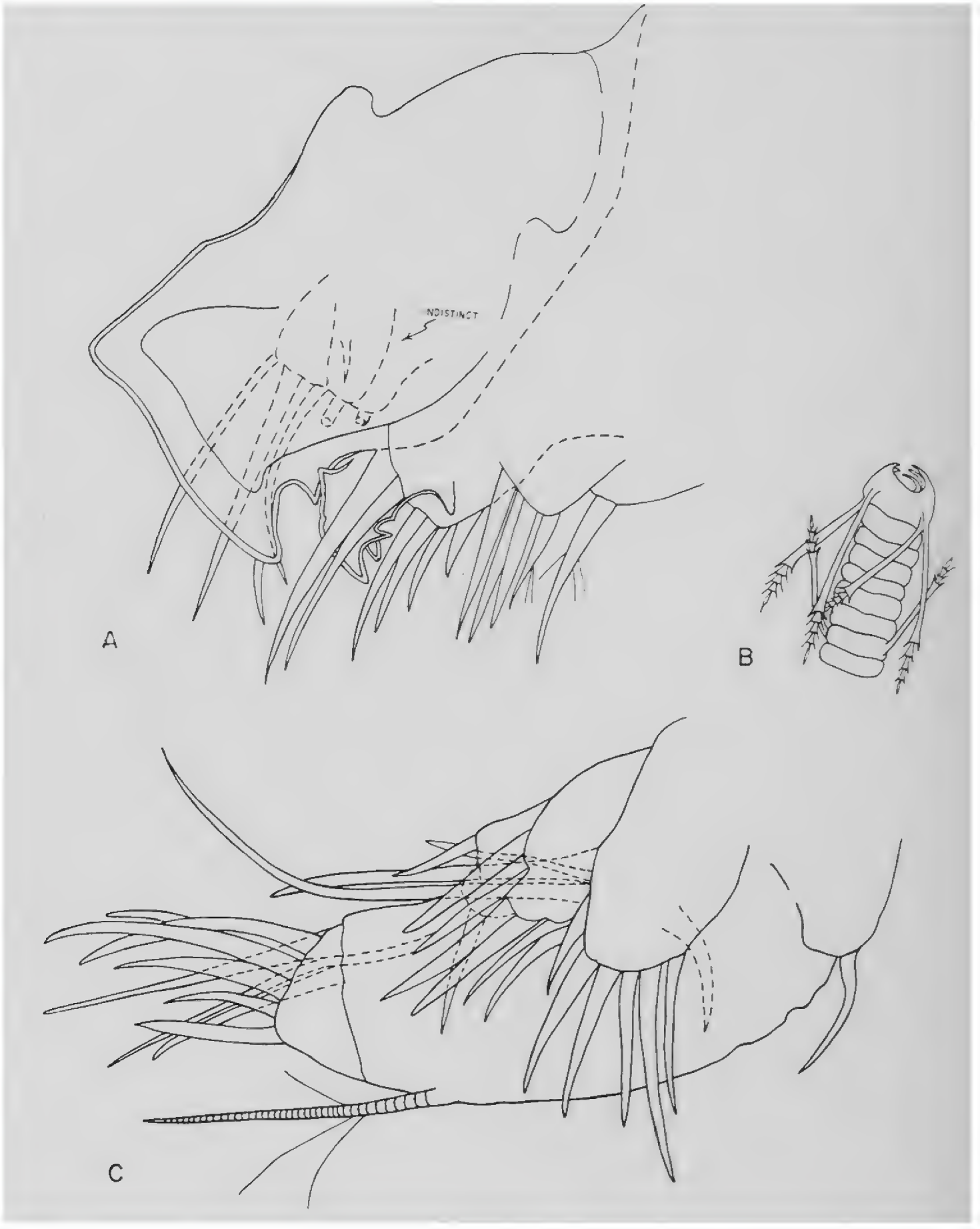

FIG. 55.

Philomedes paucichelata Kornicker, new species (Female).

A. Portion of fifth leg. Specimen No. 156–5.

B. Seventh limb. Specimen No. 156–5.

C. Portion of maxilla. Specimen No. 156–5.

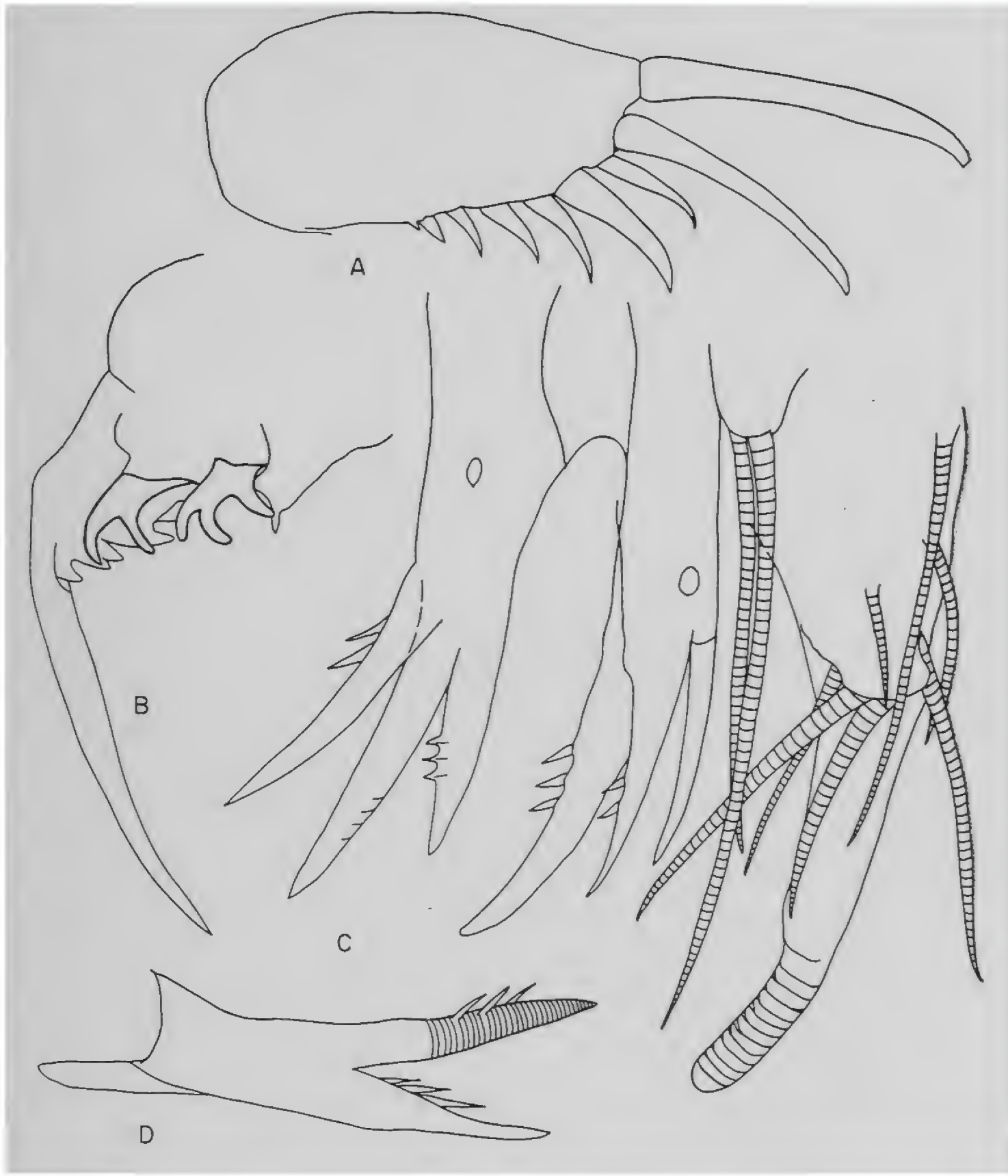

FIG. 56.

Pseudophilomedes ferulana Kornicker, new species (Female).

A. Furca. Specimen No. 118B–2.

B. Distal portion of fifth limb. Specimen No. 118B–3.

C. Distal portion of maxilla. Specimen No. 118B–3.

D. Mandibular palp. Specimen No. 118B–3.

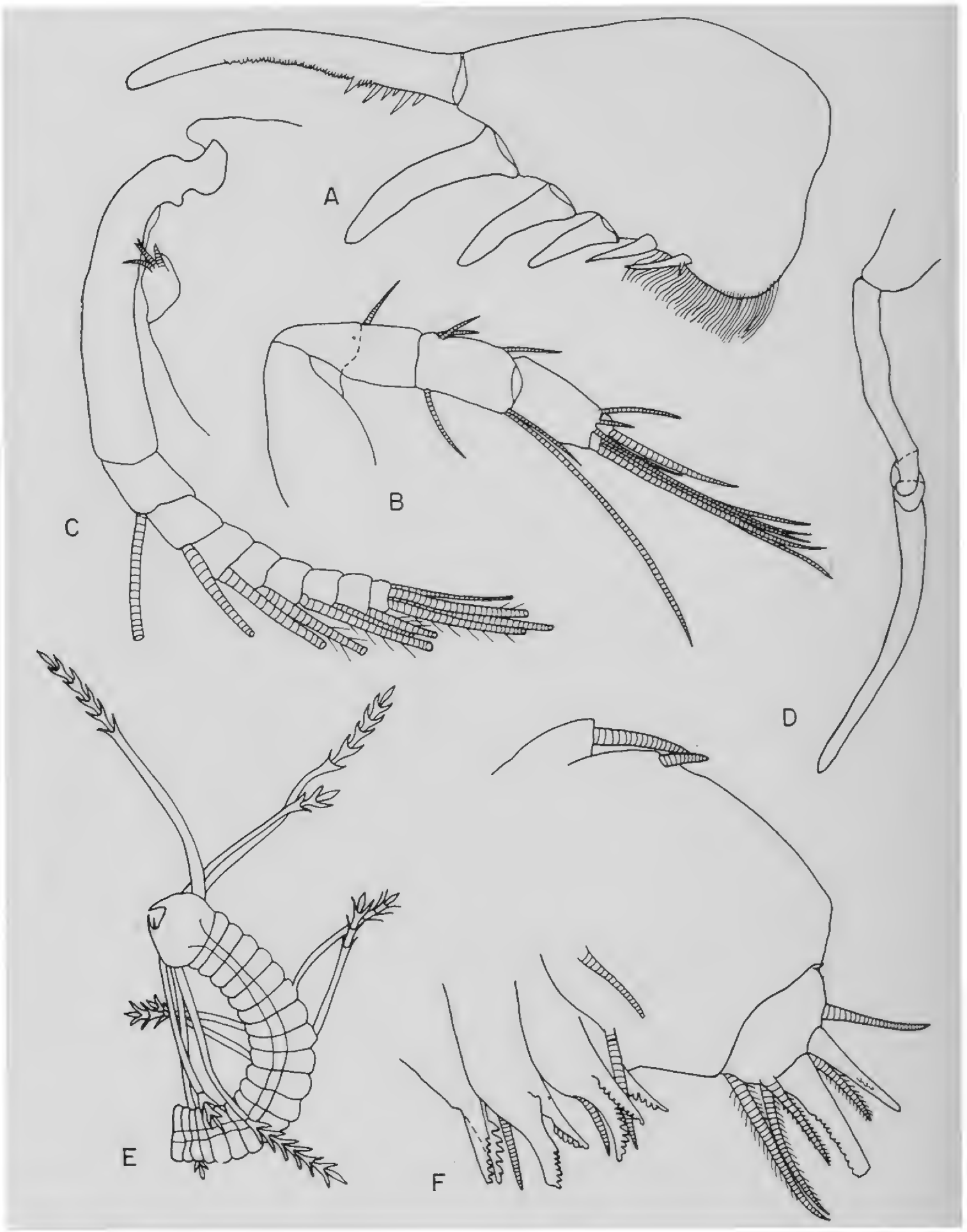

FIG. 57.

Rutiderma (Rutiderma) dinochelata Kornicker, new species (Female).

A. Furca. Specimen No. 247–10.
B. First antenna. Specimen No. 247–10.
C. Second antenna. Specimen No. 247–10.
D. Frontal organ. Specimen No. 247–10.
E. Seventh limb. Specimen No. 247–10.
F. Portion of maxilla. Specimen No. 247–10.

FIG. 58.

Rutiderma (Rutiderma) dinochelata Kornicker, new species (Female).

A. Fifth limb. Specimen No. 247–10.

B. Mandible. Specimen No. 247–10.

C. Setae of fifth limb. Specimen No. 247–10.

D. Mandible. Specimen No. 247–10.

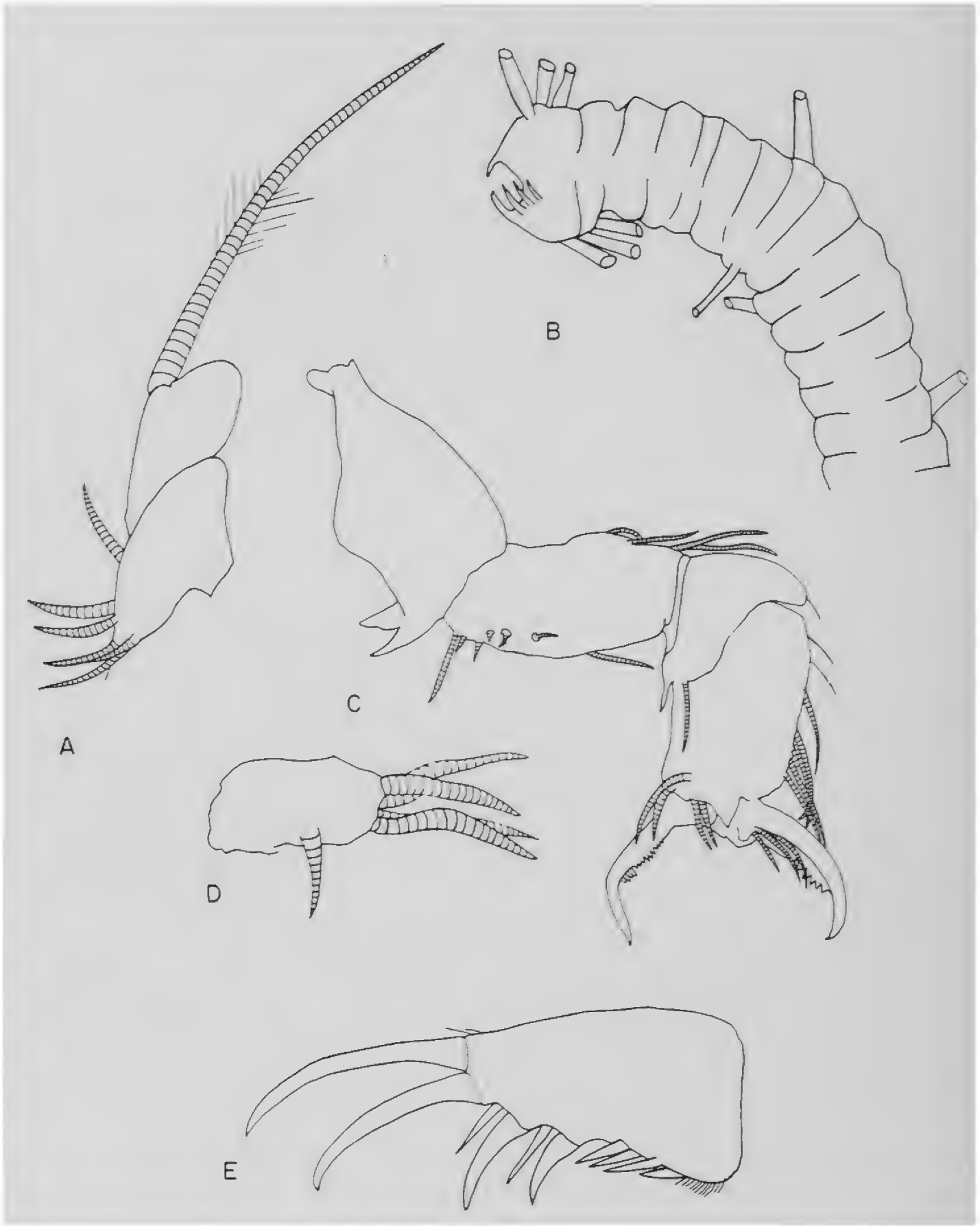

FIG. 59.

Rutiderma (Alternochelata) polychelata Kornicker, new subgenus, new species (Sex unknown).

A. Secondary branch second antenna. Specimen No. 110–2.

B. Seventh limb. Specimen No. 110–2.

C. Mandible. Specimen No. 110–2.

D. Proximal joint of secondary branch of second antenna. Specimen No. 110–2.

E. Furca. Specimen No. 110–2.

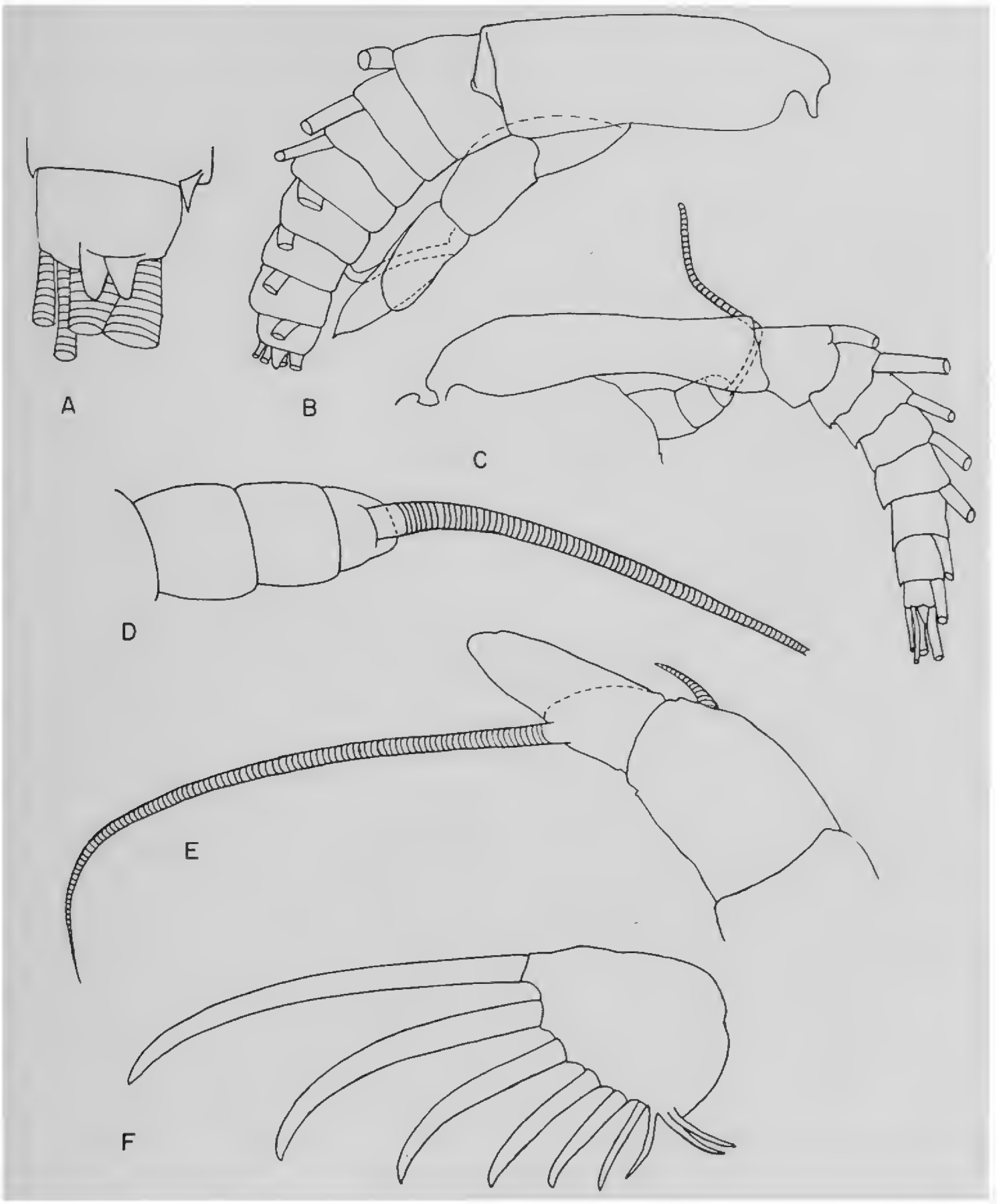

FIG. 60.

Asteropina mulleri (Skogsberg) (Sex unknown).

A. Distal end of second antenna. Specimen No. CP5–3.

B. Second antenna. Specimen No. CP5–3.

C. Second antenna. Specimen No. CPAC–1.

D. Secondary branch of second antenna. Specimen No. CPAC–1.

E. Secondary branch of second antenna. Specimen No. CP13–1.

F. Furca. Specimen No. CPAC–1.

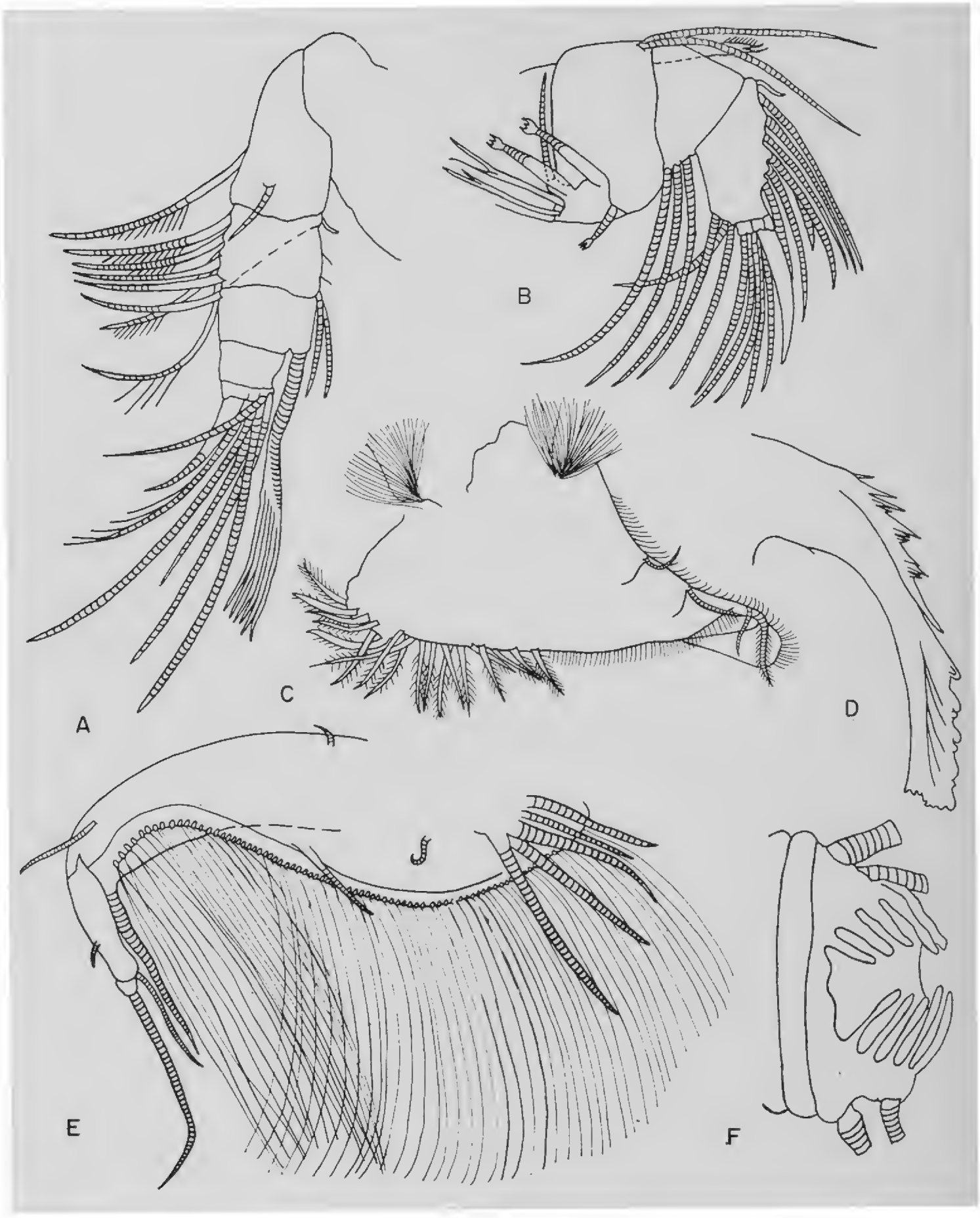

FIG. 61.

Asteropina mulleri (Skogsberg) (Female).

A. First antenna. Specimen No. CP5–1.

B. Mandible. Specimen No. CP5–1.

C. Sixth limb. Specimen No. CP5–1.

D. Mandibular process. Specimen No. CP5–1.

E. Maxilla. Specimen No. CP5–2.

F. Distal end of seventh limb. Specimen. No. CP5–2.

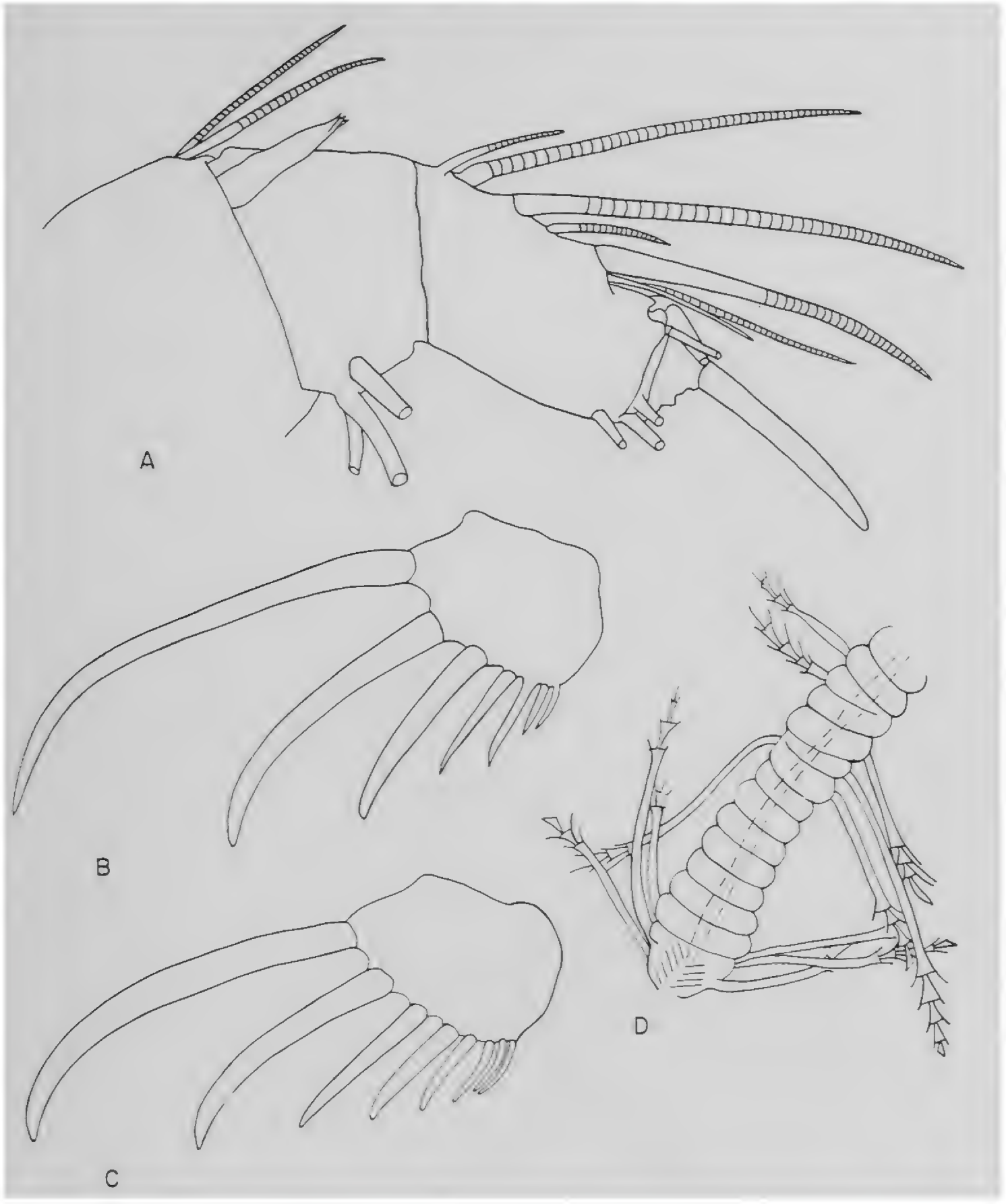

FIG. 62.

Asteropina setisparsa Kornicker, new species (Female).

A. Mandible. Specimen No. 246–3.

B. Furca. Specimen No. 120C–1.

C. Furca. Specimen No. 122D–3.

D. Seventh limb. Specimen No. 246–3.

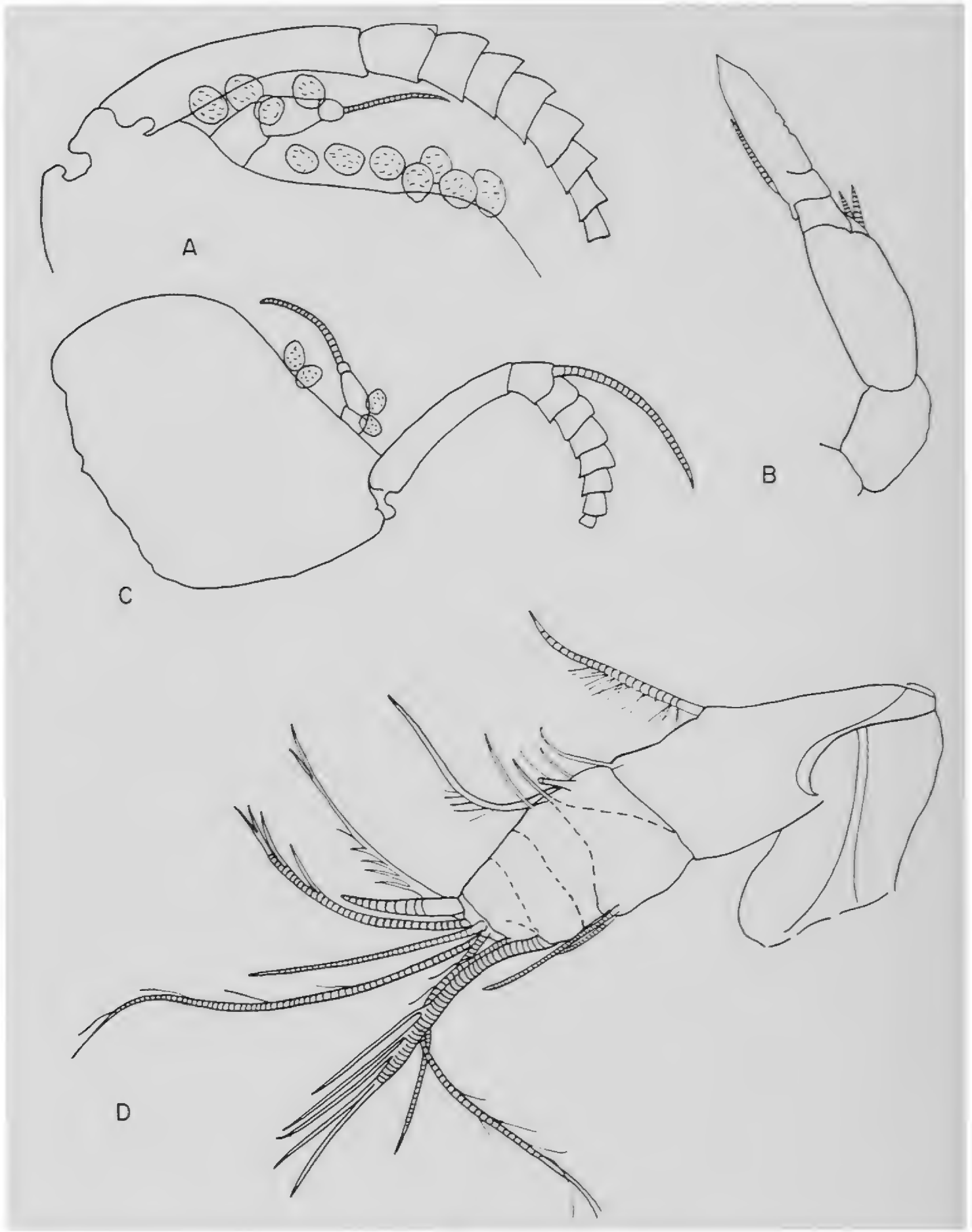

FIG. 63.

Asteropina setisparsa Kornicker, new species (Female).

A. Second antenna, sensory bristles not shown; round objects are parasites. Specimen No. 122D–3.

B. Secondary appendage of second antenna. Specimen No. 246–3.

C. Second antenna with one sensory bristle shown; round objects are parasites. Specimen No. 122D–3.

D. First antenna. Specimen No. 246–3.

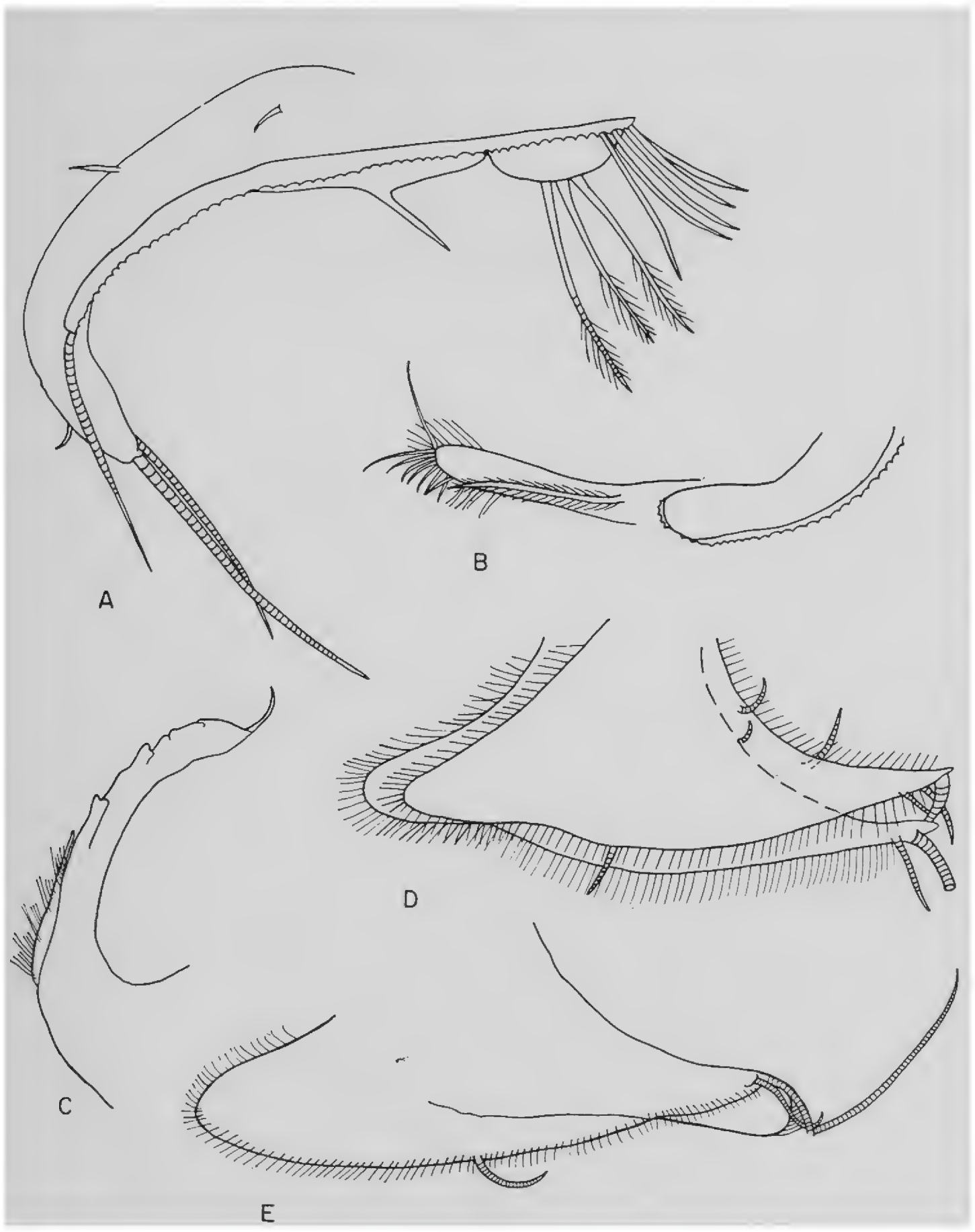

FIG. 64.

Asteropina setisparsa Kornicker, new species (Female).

A. Maxilla. Specimen No. 122D–3.

B. Fifth limb, not all setae shown. Specimen No. 122D–3.

C. Mandibular process. Specimen No. 122D–3.

D. Sixth limb. Specimen No. 122D–3.

E. Sixth limb. Specimen No. 122D–1.

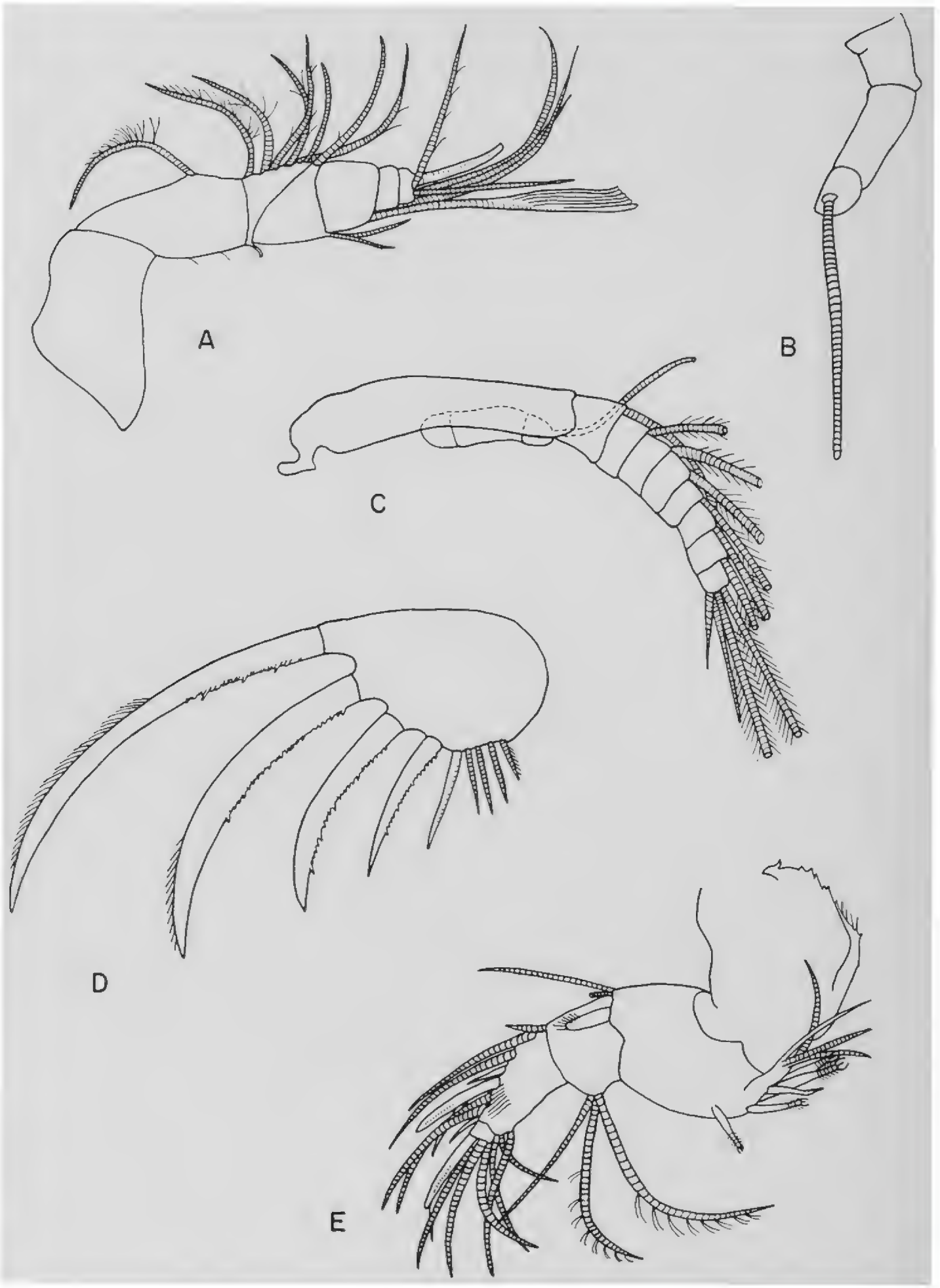

FIG. 65.

Asteropina extrachelata Kornicker, new species (Female).
A. First antenna. Specimen No. 118–1.
B. Secondary branch of second antenna. Specimen No. 118–1.
C. Second antenna. Specimen No. 118–1.
D. Furca. Specimen No. 118–1.
E. Mandible. Specimen No. 118–1.

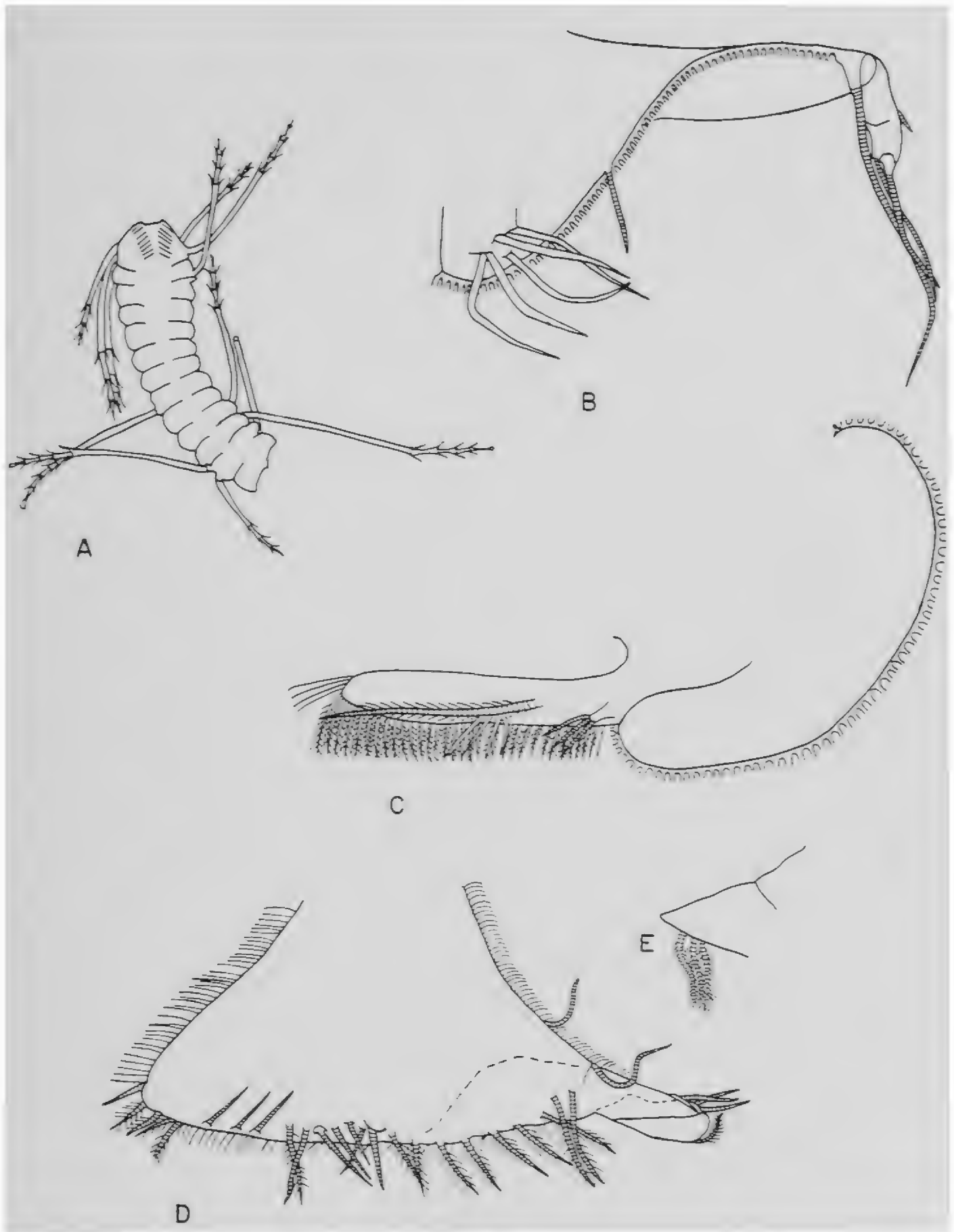

FIG. 66.

Asteropina extrachelata Kornicker, new species (Female).

A. Seventh limb. Specimen No. 118–1.
B. Maxilla. Specimen No. 118–1.
C. Fifth limb. Specimen No. 118–1.
D. Sixth limb. Specimen No. 118–1.
E. Antero-ventral corner of other sixth limb. Specimen No. 118–1.

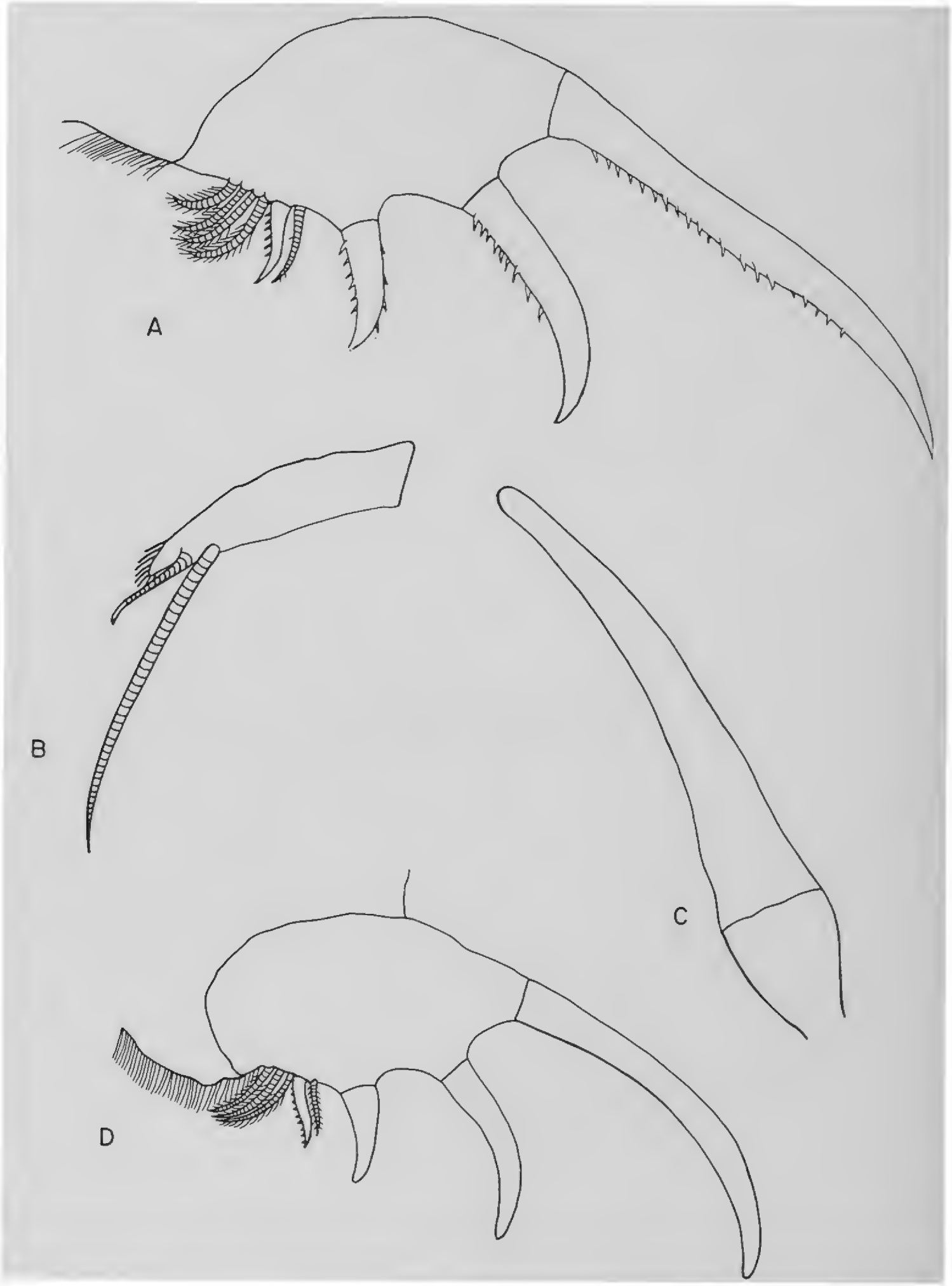

FIG. 67.

Cycloberis biminiensis Kornicker, new species (?Female).
A. Furca. Specimen No. 177–1.
B. Falciform process on mandible. Specimen No. 177–1.
C. Frontal organ. Specimen No. 177–1.
D. Furca. Specimen No. 177–2.

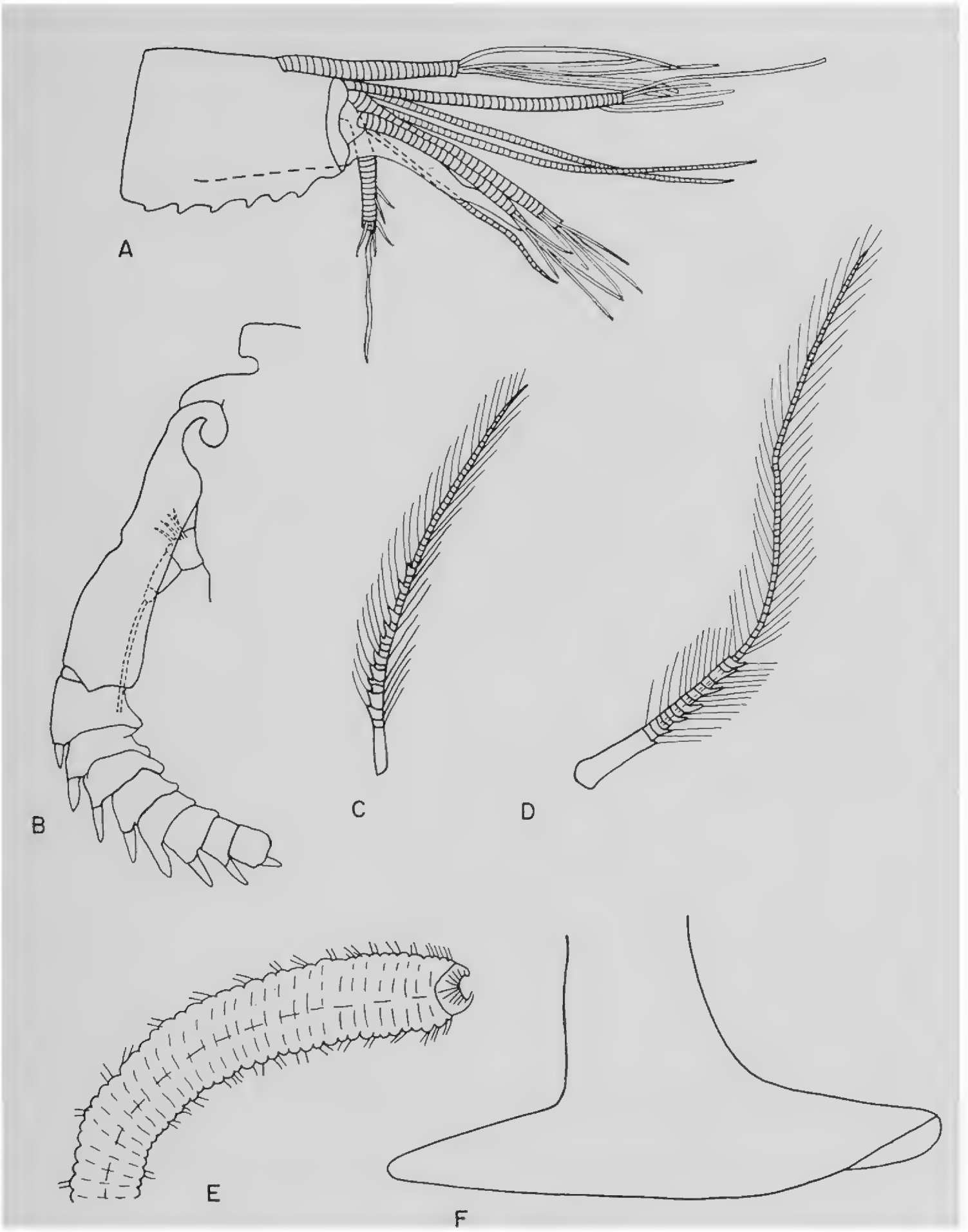

FIG. 68.

Cycloberis biminiensis Kornicker, new species (?Female).

A. Distal end first antenna. Specimen No. 177–1.
B. Second antenna, setae not shown. Specimen No. 177–1.
C. Bristle from third joint of second antenna. Specimen No. 177–2.
D. Bristle from third joint of second antenna. Specimen No. 177–1.
E. Seventh limb, stumps only shown of setae. Specimen No. 177–1.
F. Outline of sixth limb without bristles. Specimen No. 177–2.

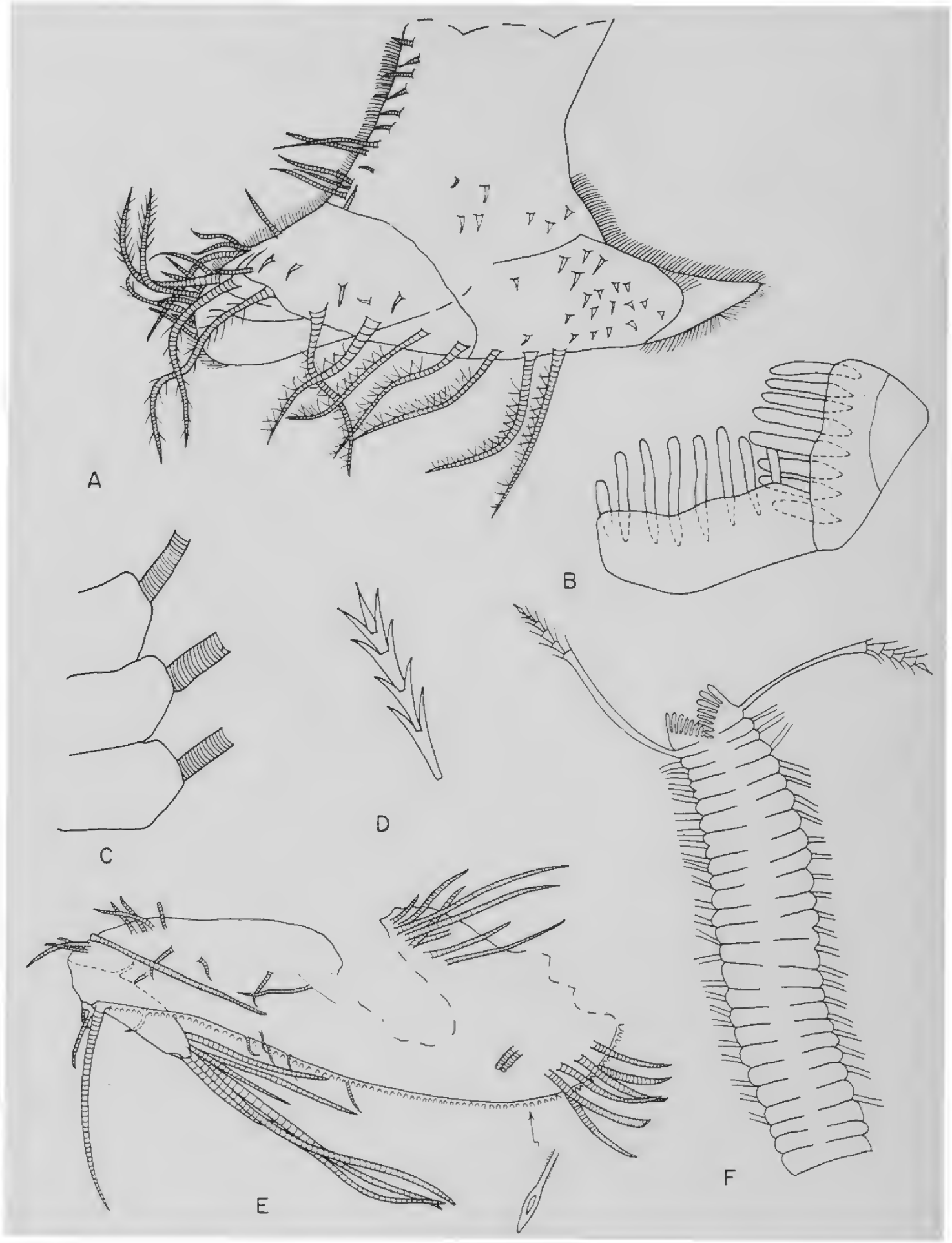

FIG. 69.

Actinoseta chelisparsa Kornicker, new genus, new species (Female).

A. Sixth limb. Specimen No. CP38–2.
B. Distal end of seventh limb. Specimen No. CP38–2.
C. Portion of segments of seventh limb. Specimen No. CP38–2.
D. Distal end of setae on seventh limb. Specimen No. CP38–2.
E. Maxilla. Specimen No. CP38–2.
F. Seventh limb. Specimen No. CP38–2.

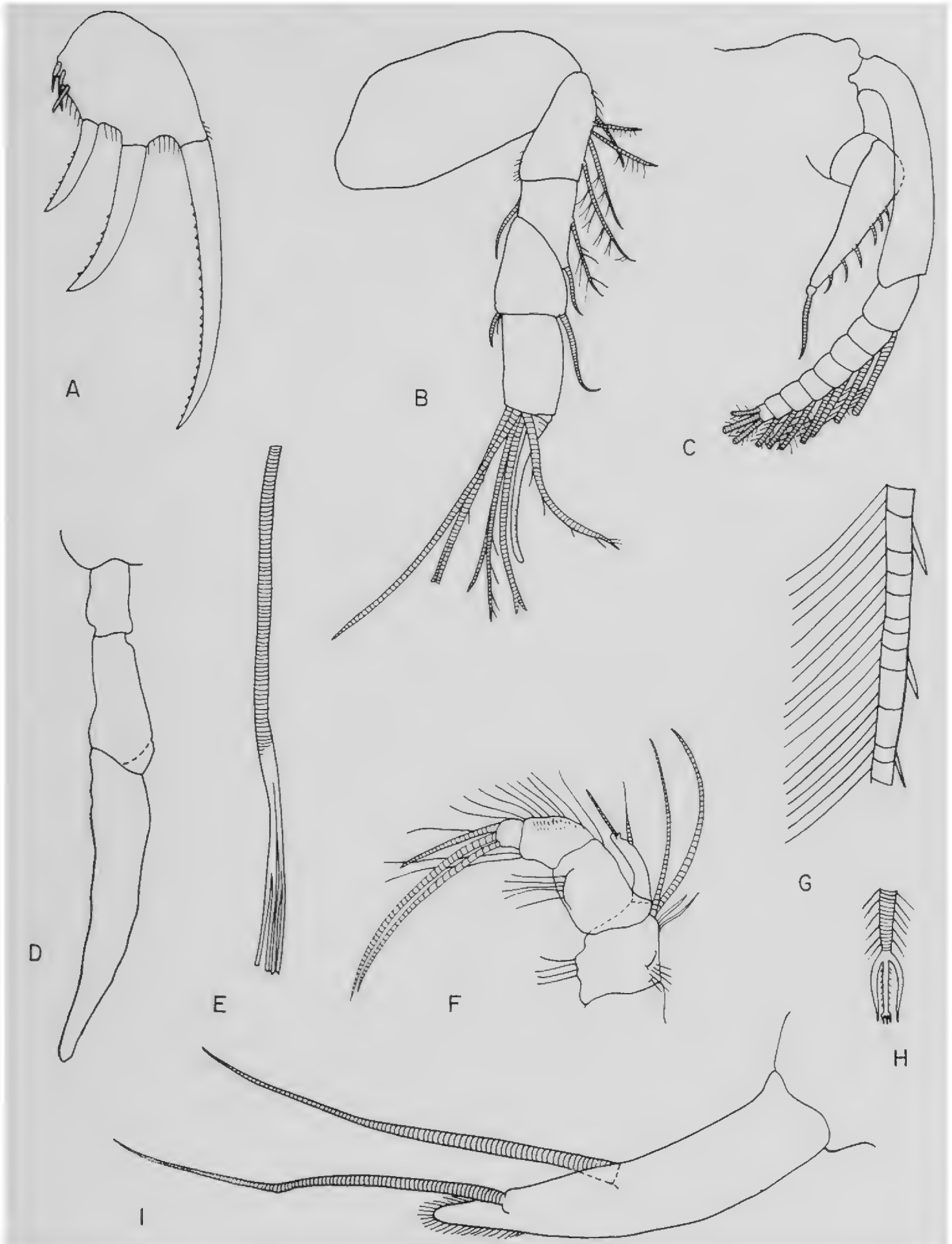

FIG. 70.

Actinoseta chelisparsa Kornicker, new species (Female).

A. Furca. Specimen No. CP52–6.
B. First antenna. Specimen No. CP38–2.
C. Second antenna. Specimen No. CP38–2.
D. Frontal organ. Specimen No. CP38–2.
E. Sensory bristle of first antenna. Specimen No. CP52–6.
F. Mandible. Specimen No. CP38–2.
G. Part of distal half of setae on second joint of second antenna. Specimen No. CP38–2.
H. Mandible bristle. Specimen No. CP38–2.
I. Falciform process on mandible. Specimen No. CP38–2.

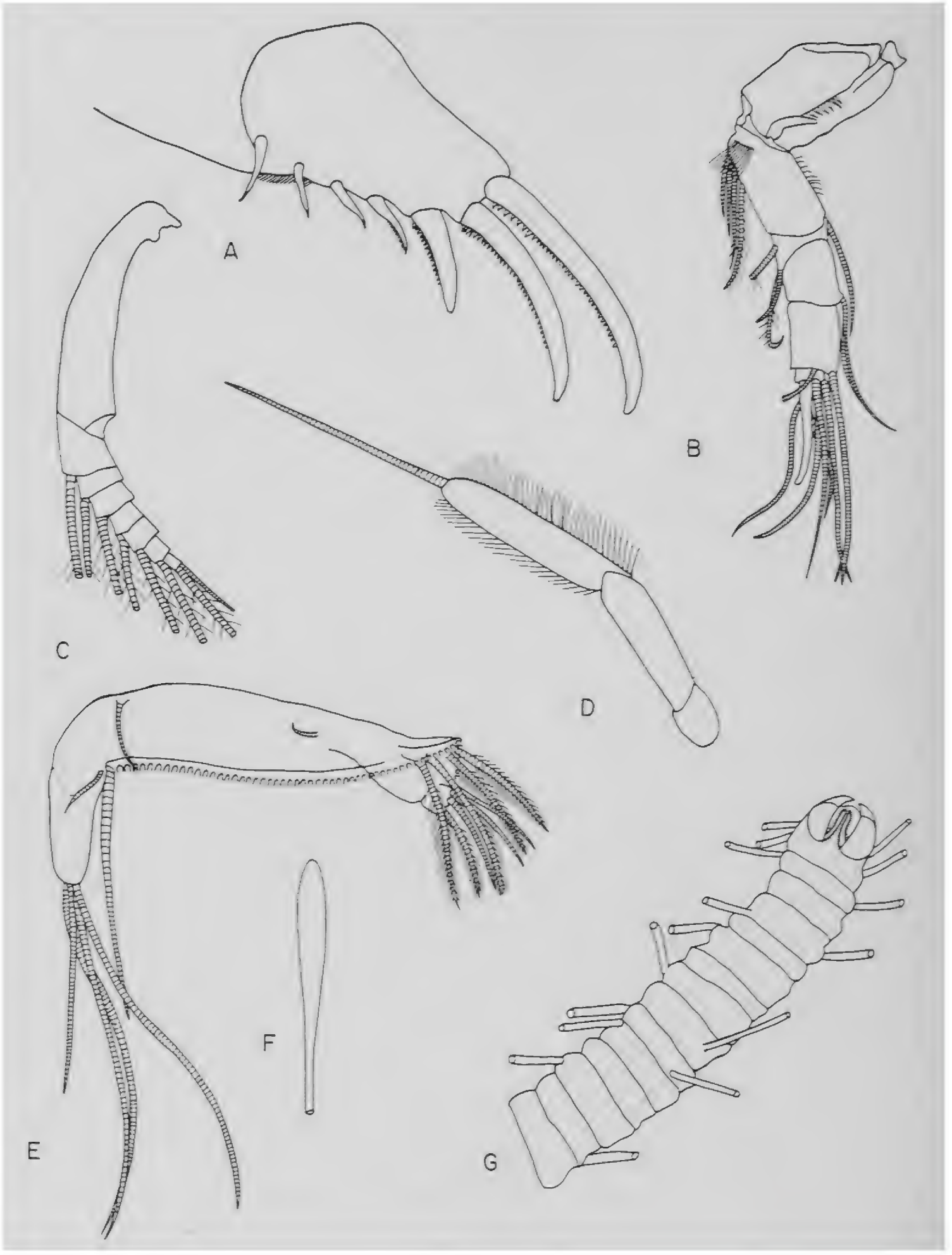

FIG. 71.

Asteropteron monambon Kornicker, new species (Female).

A. Furca. Specimen No. CP52–4.
B. First antenna. Specimen No. CP52–4.
C. Second antenna. Specimen No. CP52–4.
D. Secondary branch of second antenna. Specimen No. CP52–4.
E. Maxilla. Specimen No. CP52–4.
F. Paddle-shaped tip of maxillary bristle. Specimen No. CP52–4.
G. Seventh limb. Specimen No. CP52–4.

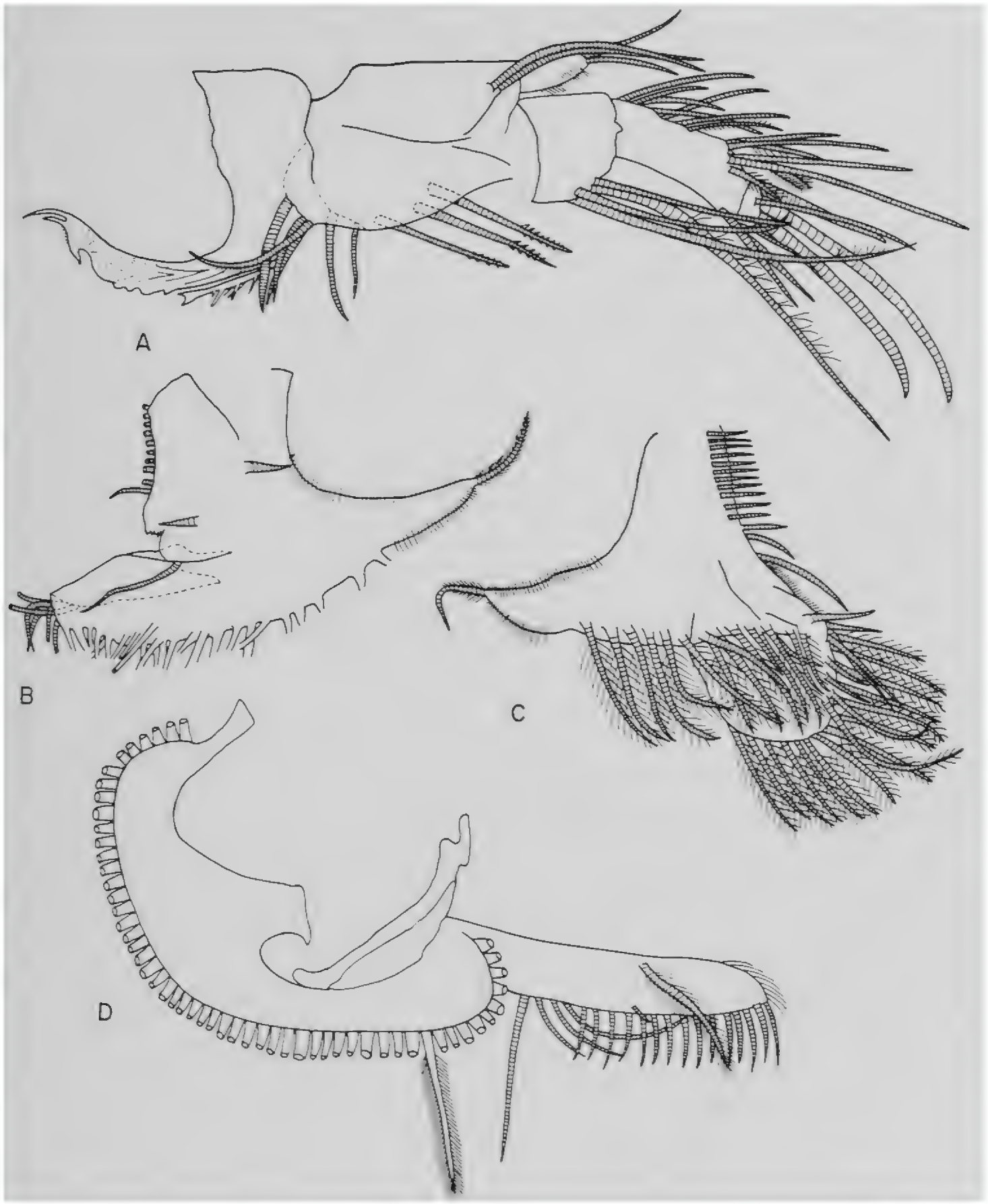

FIG. 72.

Asteropteron monambon Kornicker, new species (Female).

A. Mandible. Specimen No. CP52–4.

B. Sixth limb. Specimen No. CP52–4.

C. Sixth limb. Specimen No. CP52–4.

D. Fifth limb. Specimen No. CP52–4.

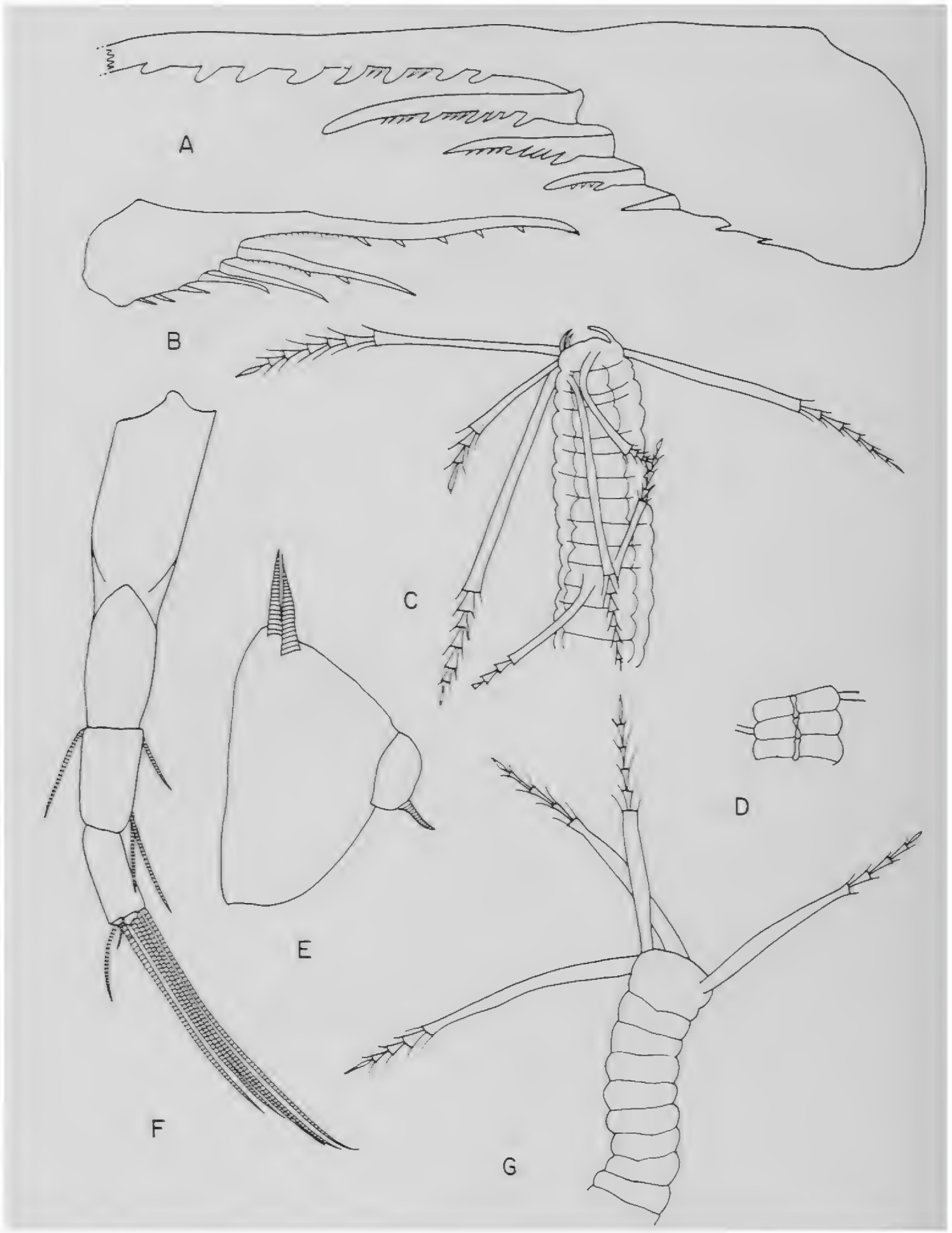

FIG. 73.

Sarsiella carinata A. Scott (Female).

A. Furca. Specimen No. CP38–13.
B. Furca. Specimen No. CP38–5.
C. Seventh limb. Specimen No. CP38–13.
D. Portion of seventh limb (mate of C). Specimen No. CP38–13.
E. Secondary branch first antenna. Specimen No. CP38–5.
F. First antenna. Specimen CP38–5.
G. Seventh limb. Specimen No. CP38–5.
Note: Specimen No. CP38–5 is young instar.
Specimen No. CP38–13 is mature.

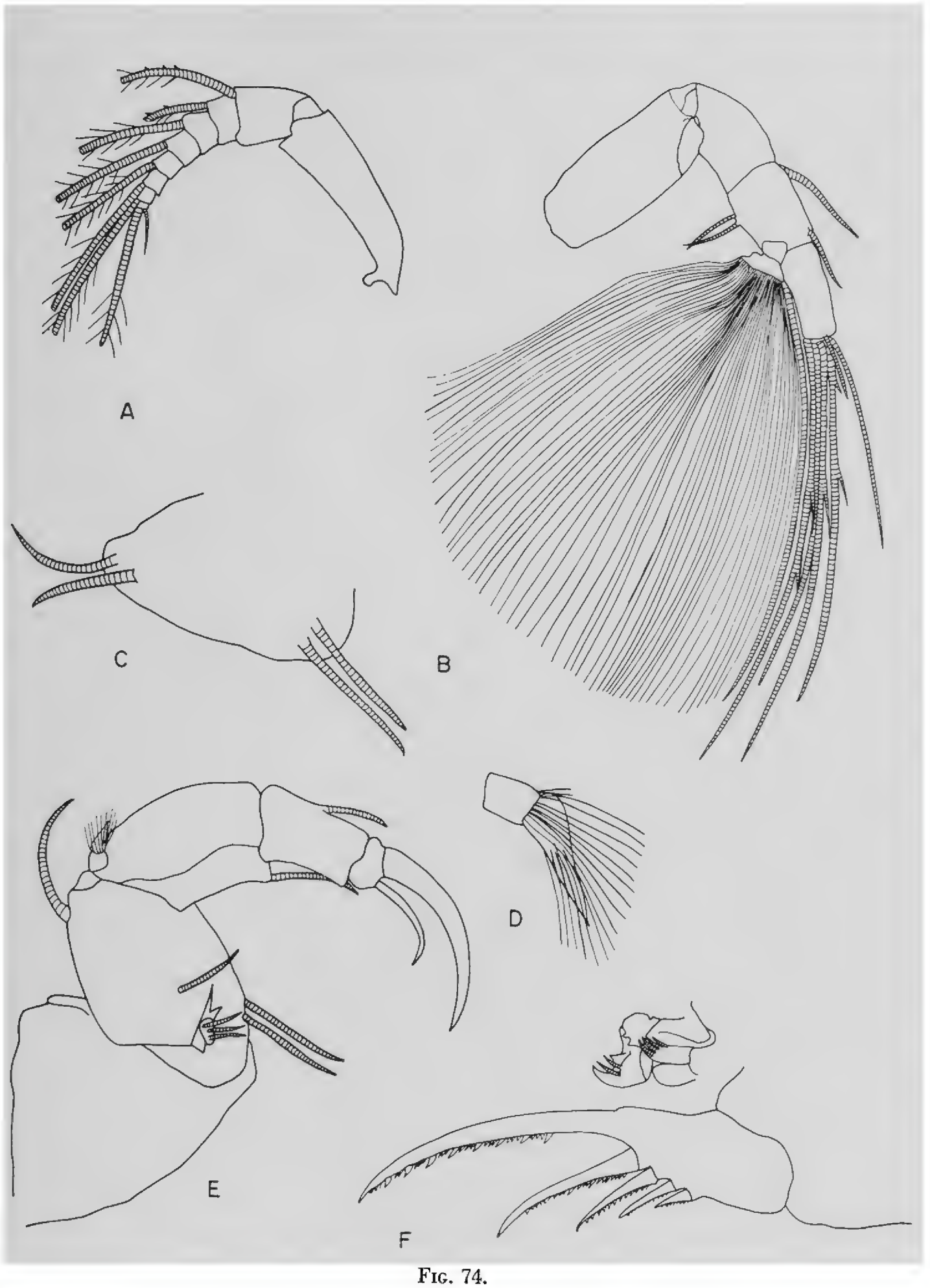

FIG. 74.

Sarsiella carinata A. Scott (Male).

A. Second antenna. Specimen No. CP52–23.
B. First antenna. Specimen No. CP52–23.
C. Secondary branch of second antenna. Specimen No. CP52–23.
D. Process on mandible. Specimen No. CP52–23.
E. Mandible. Specimen No. CP52–23.
F. Furca and penis. Specimen No. CP52–23.

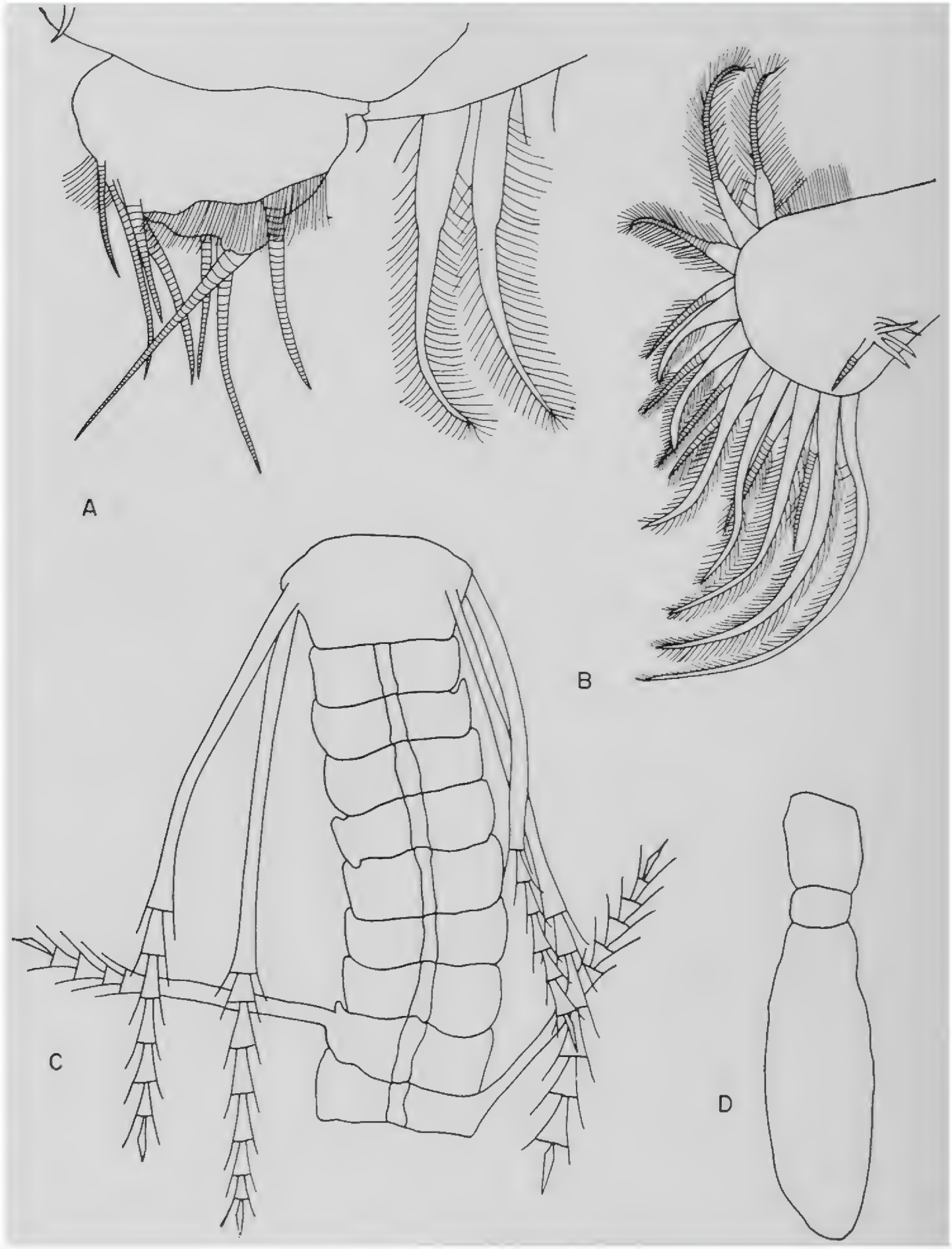

FIG. 75.

Sarsiella carinata A. Scott (Male).
A. Fifth limb. Specimen No. CP52–23.
B. Sixth limb. Specimen No. CP52–23.
C. Seventh limb. Specimen No. CP52–23.
D. Frontal organ. Specimen No. CP52–23.

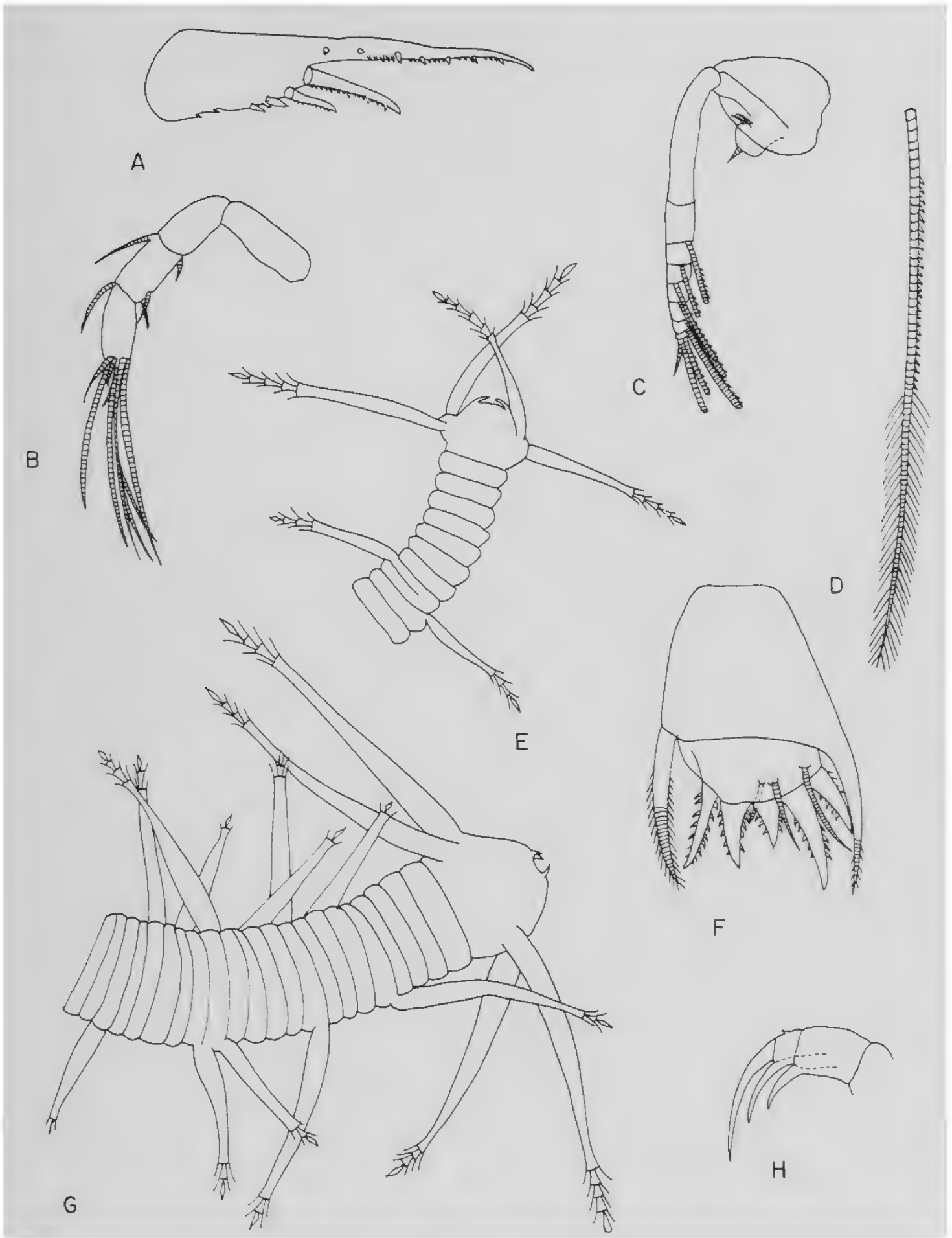

FIG. 76.

Sarsiella capillaris Kornicker, new species (Female).

A. Furca. Specimen No. CP38–10.
B. First antenna. Specimen No. CP38–10.
C. Second antenna. Specimen No. CP38–10.
D. Detail of bristle on seventh joint of second antenna. Specimen No. CP38–10.
E. Seventh limb. Specimen No. CP38–10.
F. Maxilla. Specimen No. CP38–10.
H. Distal end of mandible. Specimen No. CP38–10.

Sarsiella gigacantha Kornicker, new species (Female).

G. Seventh limb. Specimen No. S–2.

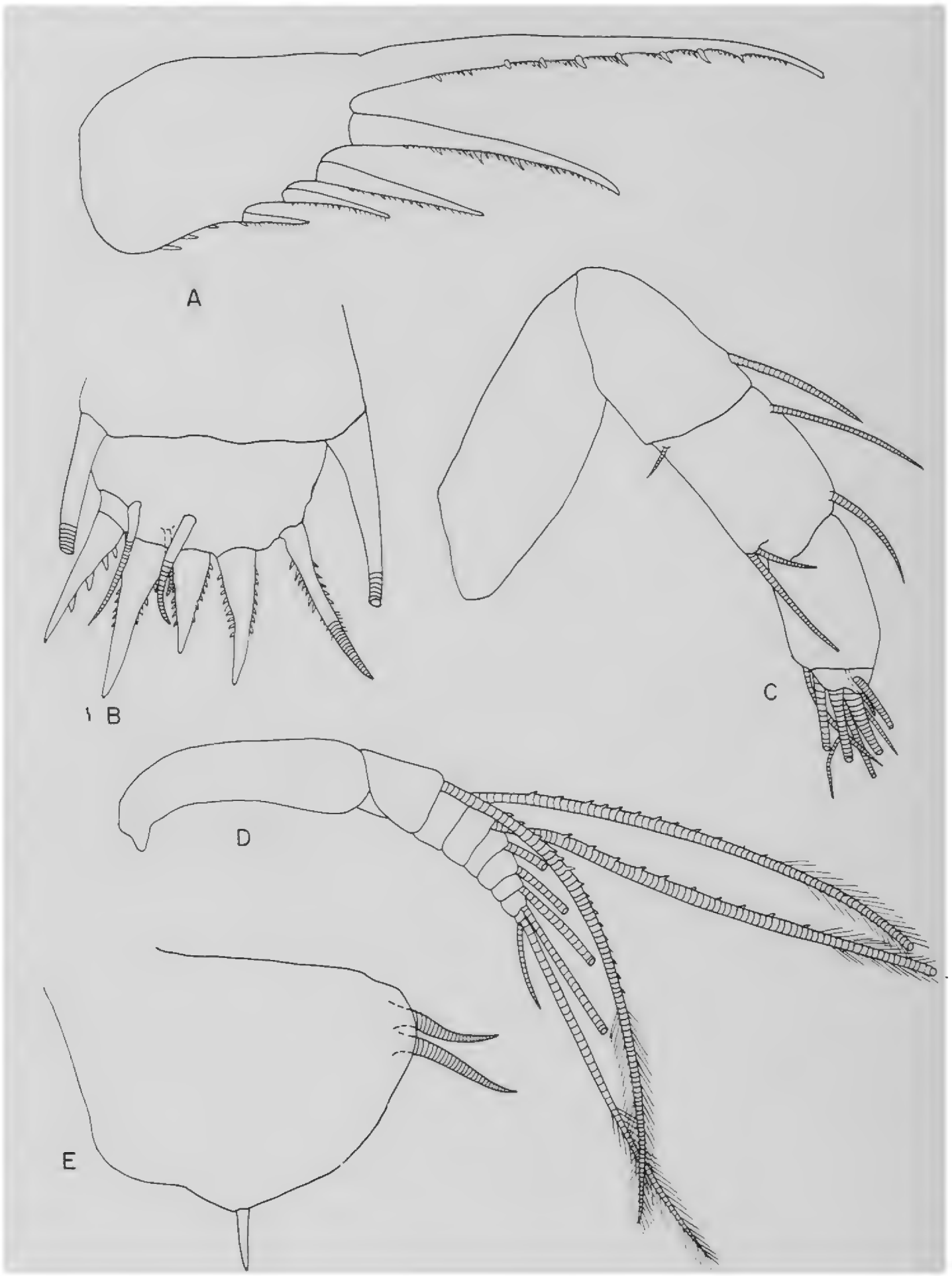

FIG. 77.

Sarsiella gigacantha Kornicker, new species (Female).

A. Furca. Specimen No. S–2.

B. Maxilla. Specimen No. S–2.

C. First antenna. Specimen No. S–2.

D. Second antenna. Specimen No. S–2.

E. Secondary branch of second antenna. Specimen No. S–2.

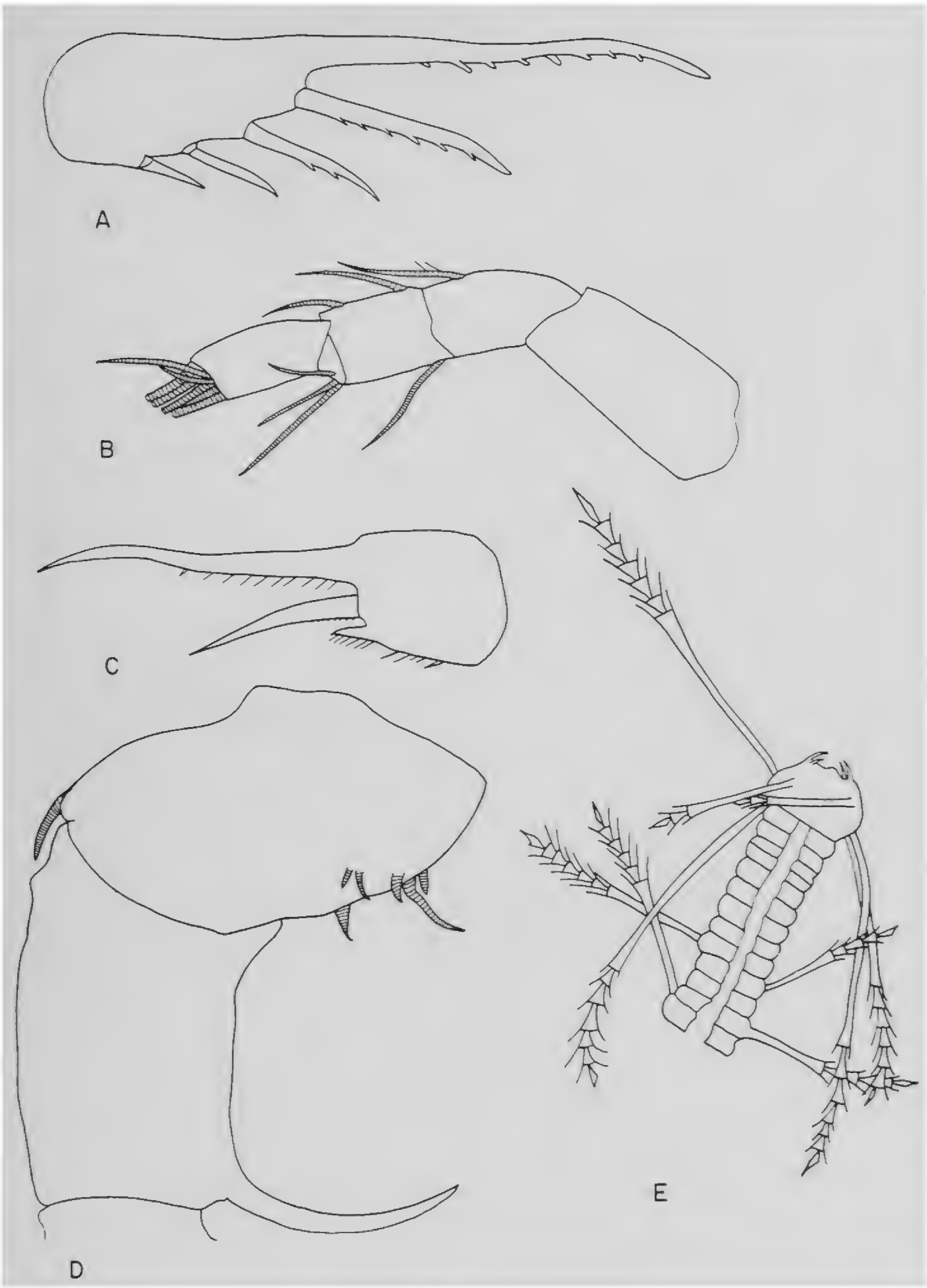

FIG. 78.

Sarsiella truncana Kornicker, new species (Female).

A. Furca. Specimen No. CP52–21.

B. First antenna. Specimen No. CP52–21.

C. Furca (young instar). Specimen No. CP38–6.

D. Part of mandible. Specimen No. CP52–21.

E. Seventh limb. Specimen No. CP52–20.

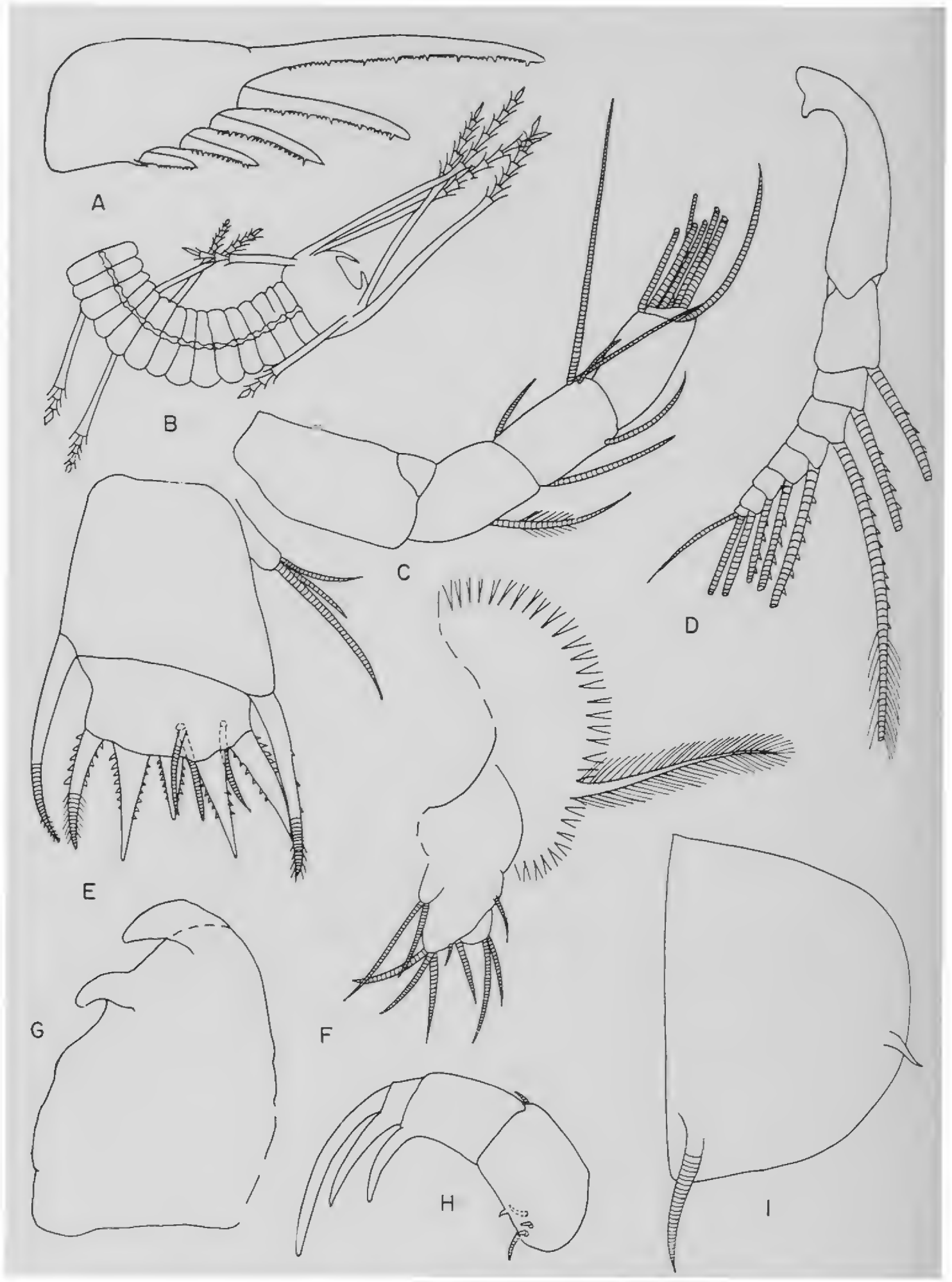

FIG. 79.

Sarsiella punctata Kornicker, new species.

A. Furca. Specimen No. CP38–9.
B. Seventh limb. Specimen No. CP38–9.
C. First antenna. Specimen No. CP38–9.
D. Second antenna. Specimen No. CP38–9.
E. Maxilla. Specimen No. CP38–9.
F. Fifth limb. Specimen No. CP38–9.
G. Penis. Specimen No. 119A–1.
H. Mandible. Specimen No. CP38–9.
I. Secondary branch of second antenna. Specimen No. CP38–9.
Note: Specimen No. CP38–9 is male.
Specimen No. 119A–1 is female.

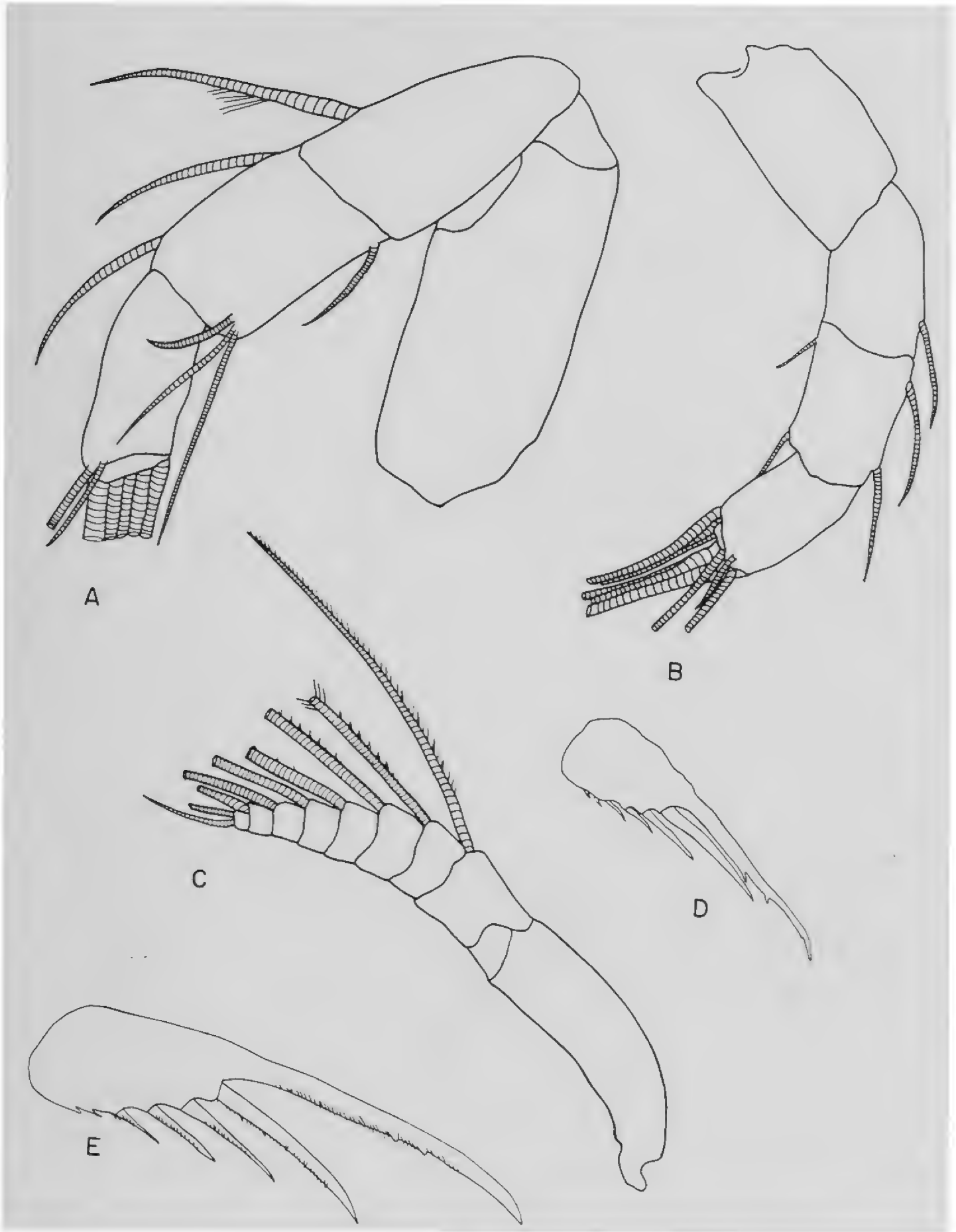

FIG. 80.

Sarsiella costata Kornicker, new species (Female).

A. First antenna. Specimen No. CP52–19.
B. First antenna. Specimen No. CP38–8.
C. Second antenna. Specimen No. CP38–8.
D. Furca. Specimen No. CP38–8.
E. Furca. Specimen No. CP52–19.
Note: Specimen No. CP38–8 is young instar.
Specimen No. CP52–19 is mature.

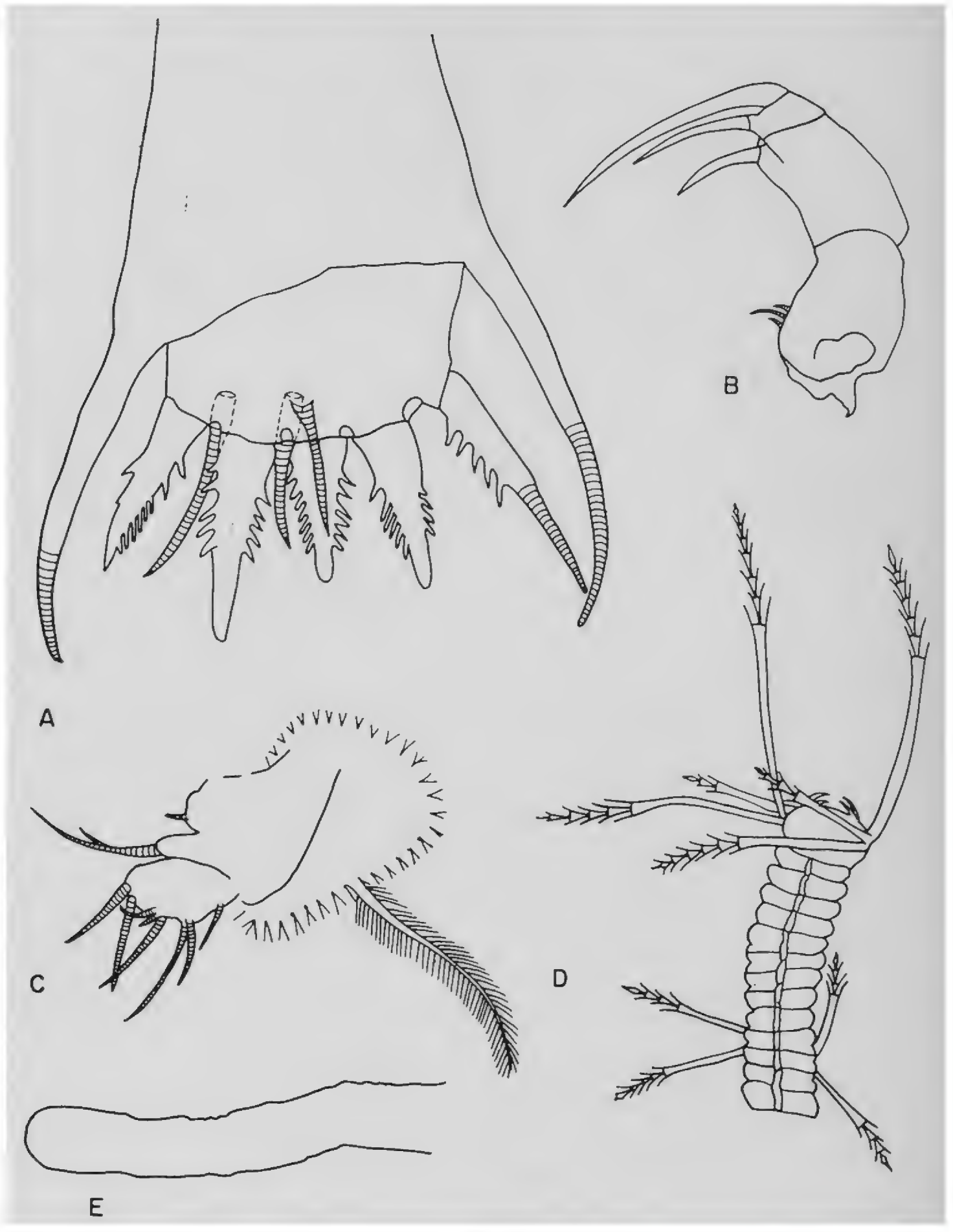

FIG. 81

Sarsiella costata Kornicker, new species (Female).

A. Maxilla. Specimen No. CP38–8.
B. Mandible. Specimen No. CP38–8.
C. Fifth limb. Specimen No. CP38–8.
D. Seventh limb. Specimen No. CP52–19.
E. Seventh limb. Specimen No. CP38–8.

Note: Specimen No. CP38–8 is young instar.
Specimen No. CP52–19 is mature.

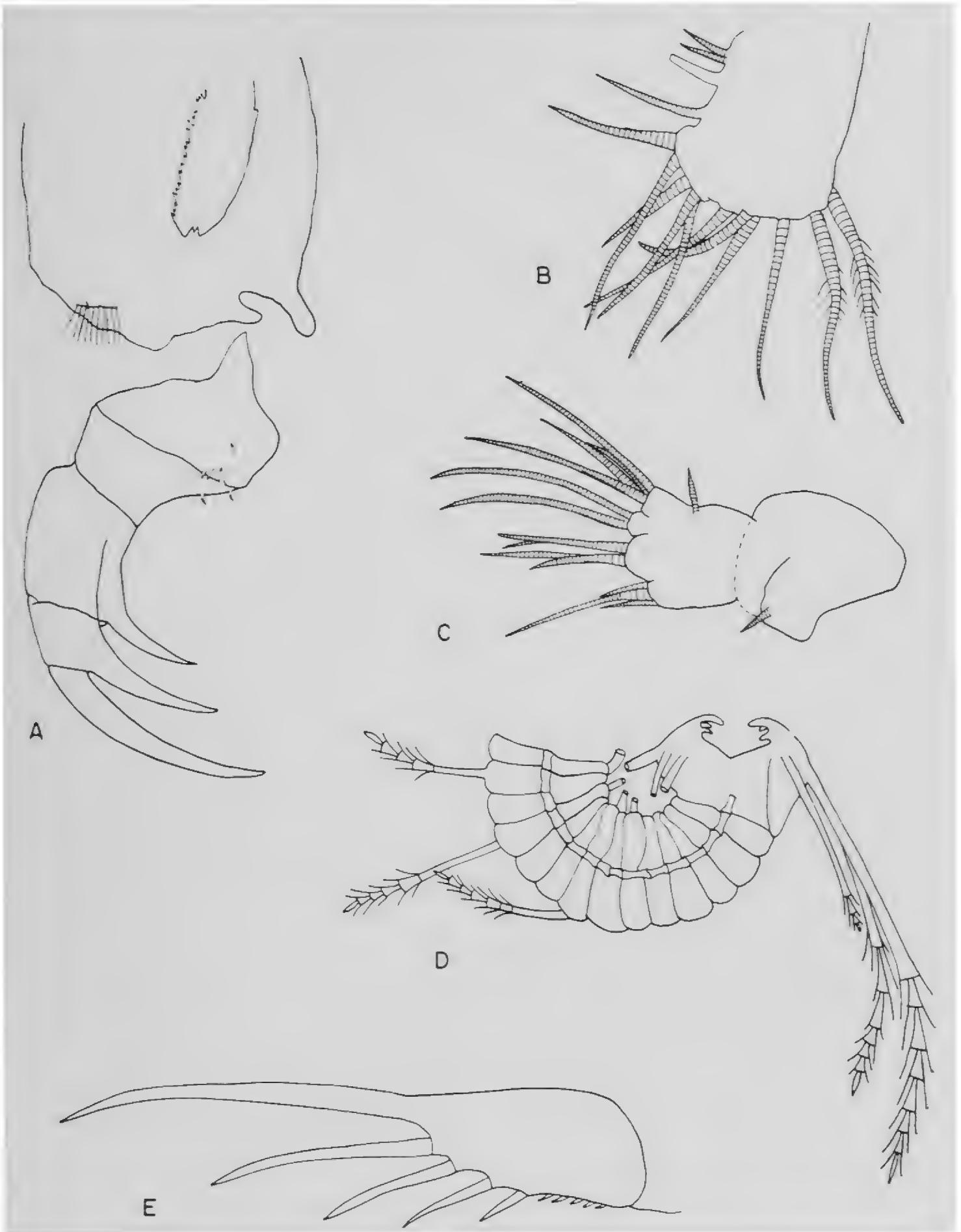

FIG. 82.

Chelicopia arostrata Kornicker, new genus, new species (Female).

A. Mandible. Specimen No. CP38–16.

B. Sixth limb. Specimen No. CP38–16.

C. Fifth limb. Specimen No. CP38–16.

Sarsiella sculpta Brady (Female).

D. Seventh limb. Specimen No. 177–1.

E. Furca. Specimen No. 177–1.

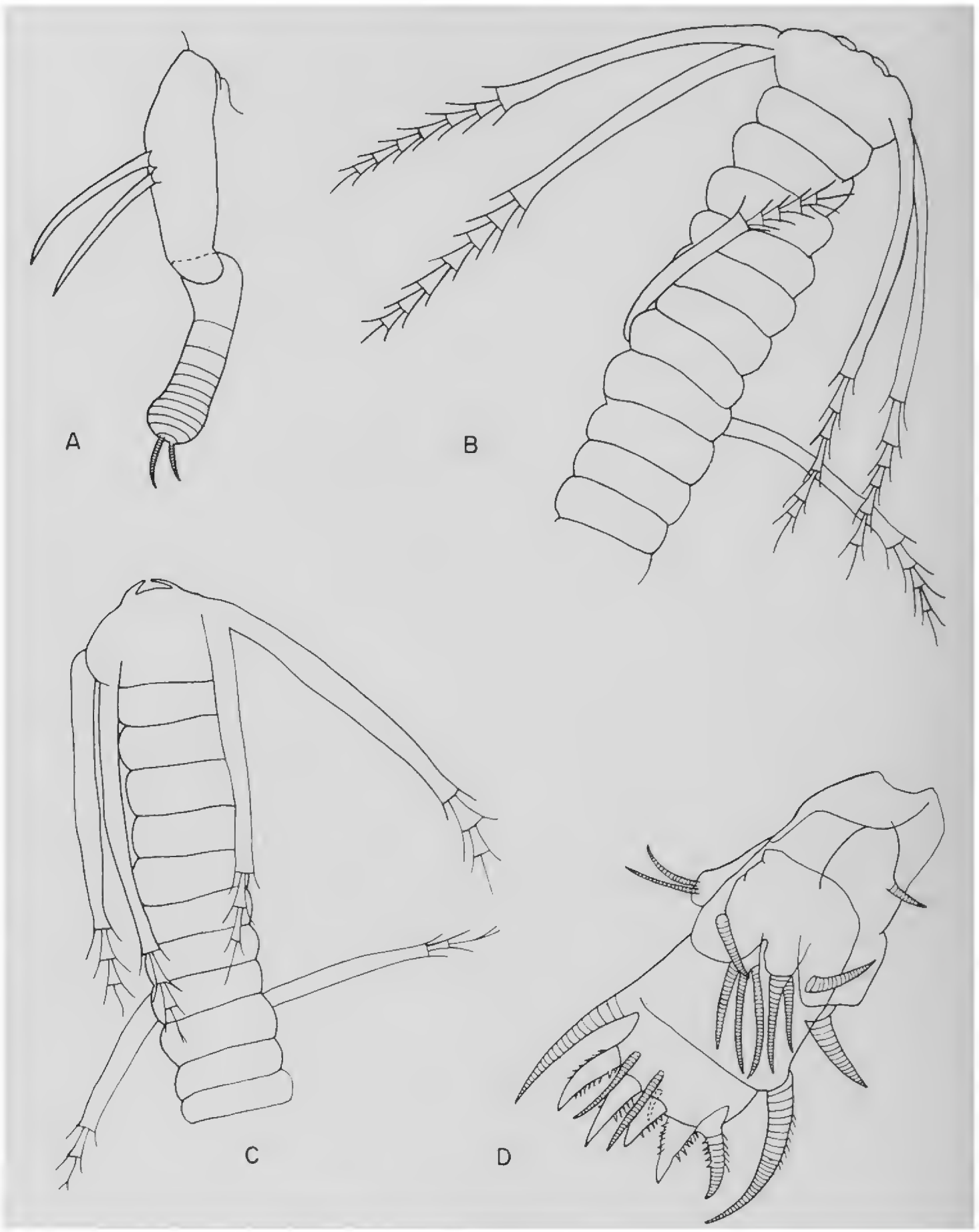

FIG. 83.

Chelicopia arostrata Kornicker, new genus, new species (Male).

A. Secondary branch of second antenna. Specimen No. 118A–1.

B. Seventh limb. Specimen No. 118A–1.

Chelicopia arostrata Kornicker (Female).

C. Seventh limb. Specimen No. CP38-16.

D. Maxilla. Specimen No. CP38–16.

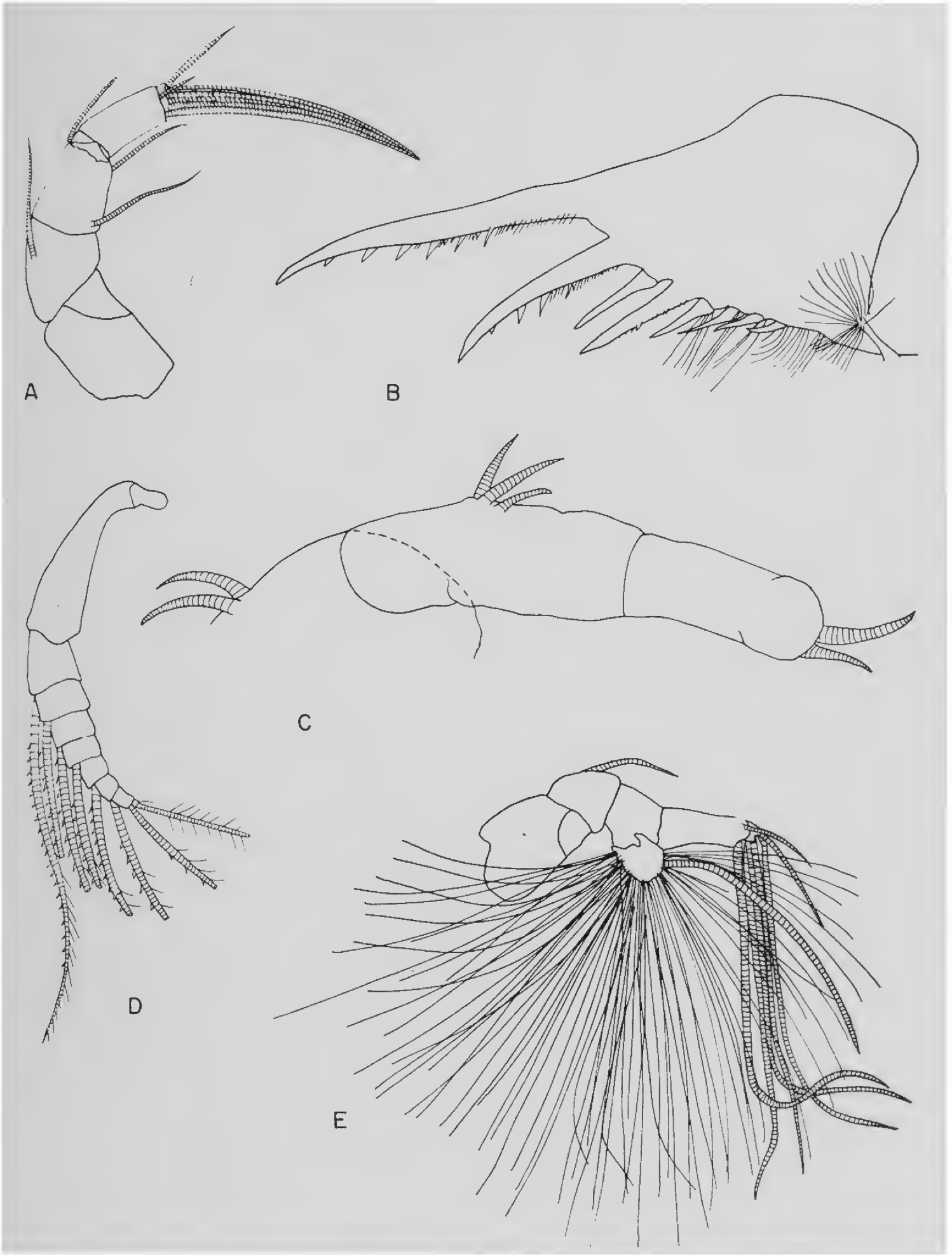

FIG. 84.

Chelicopia arostrata Kornicker, new genus, new species (Female).

A. First antenna. Specimen No. CP38–16.

B. Furca. Specimen No. CP38–16.

C. Secondary branch of second antenna. Specimen No. CP38–16.

D. Second antenna. Specimen No. CP38–16.

Chelicopia arostrata Kornicker (Male).

E. First antenna. Specimen No. 118A–1.

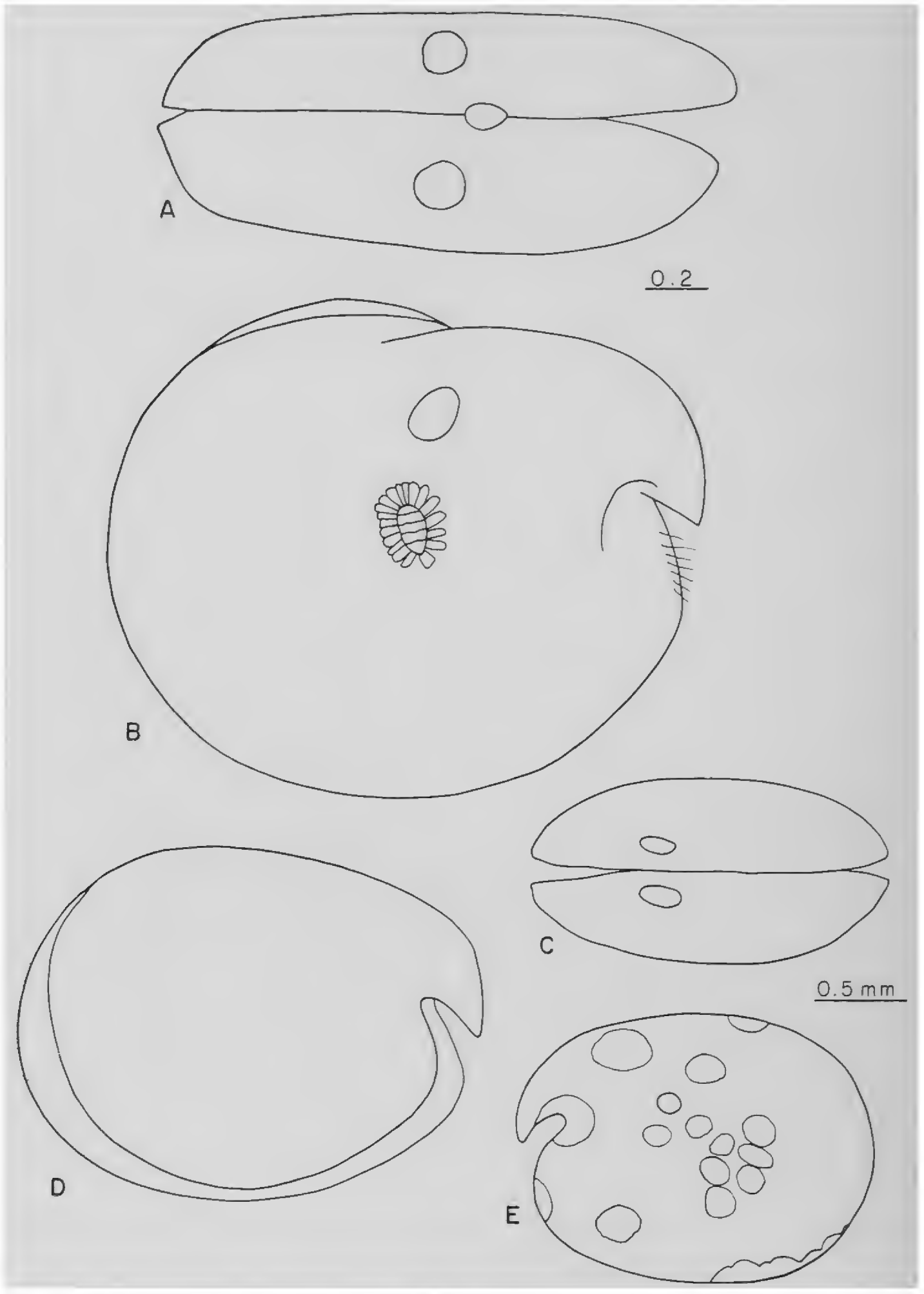

FIG. 85.

Cycloberis biminiensis Kornicker, new species

A. Dorsal view. Specimen No. 177–1.
B. Lateral view showing muscle scar. Crease on dorsal edge occurred after death. Specimen No. 177–1.
C. Dorsal view. Specimen No. 156–1.
D. Lateral outline. Specimen No. 177–2.
E. Lateral outline. Specimen No. 156–1. Spots on shell occurred after death.

Note: The shells of the species are soft and the above figured shells are somewhat misshapen.
Figures with similar magnification, A, B, D; C, E.

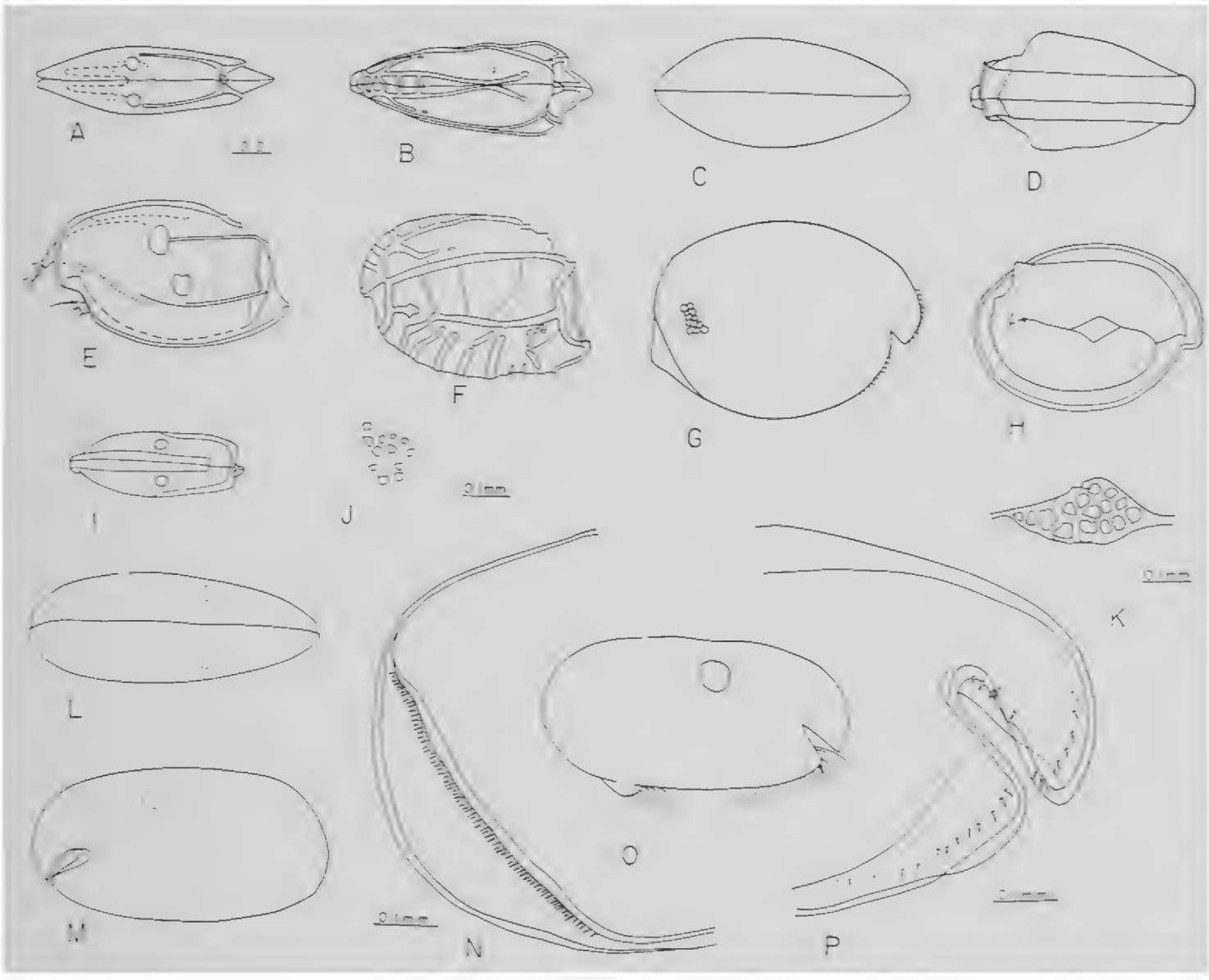

FIG. 86.

A, E, I. *Philomedes lomae* (Juday), male. A, Dorsal view (shell slightly tilted anteriorly); E, side view. Specimen No. CP52–12. I, Dorsal view Specimen No. CP–3.

B, F, J. *Rutiderma (Rutiderma)* donochelata Kornicker, new species, female. B, Dorsal view; F, Side view; J, Surface pits. Specimen No. 91–1.

C, G. *Rutiderma (Alternochelata) polychelata* Kornicker, new subgenus, new species, female. C, Dorsal view; G, Side view. Specimen No. 110F–2.

D, H, K. *Asteropteron monambon* Kornicker, new species, female. D, Dorsal view: H. Side view; K, Detail of central boss. Specimen No. 243–1.

L, P. *Asteropina setisparsa* Kornicker, new species, female. L, Dorsal view: M, Side view. Specimen No. 127–G1. N, Inside view posterior end. P, Inside view anterior end. Specimen No. 122D–1. O, Side view. Specimen No. 246–3. Figures with similar magnification, A-I, L, M, O: J, K: N, P.

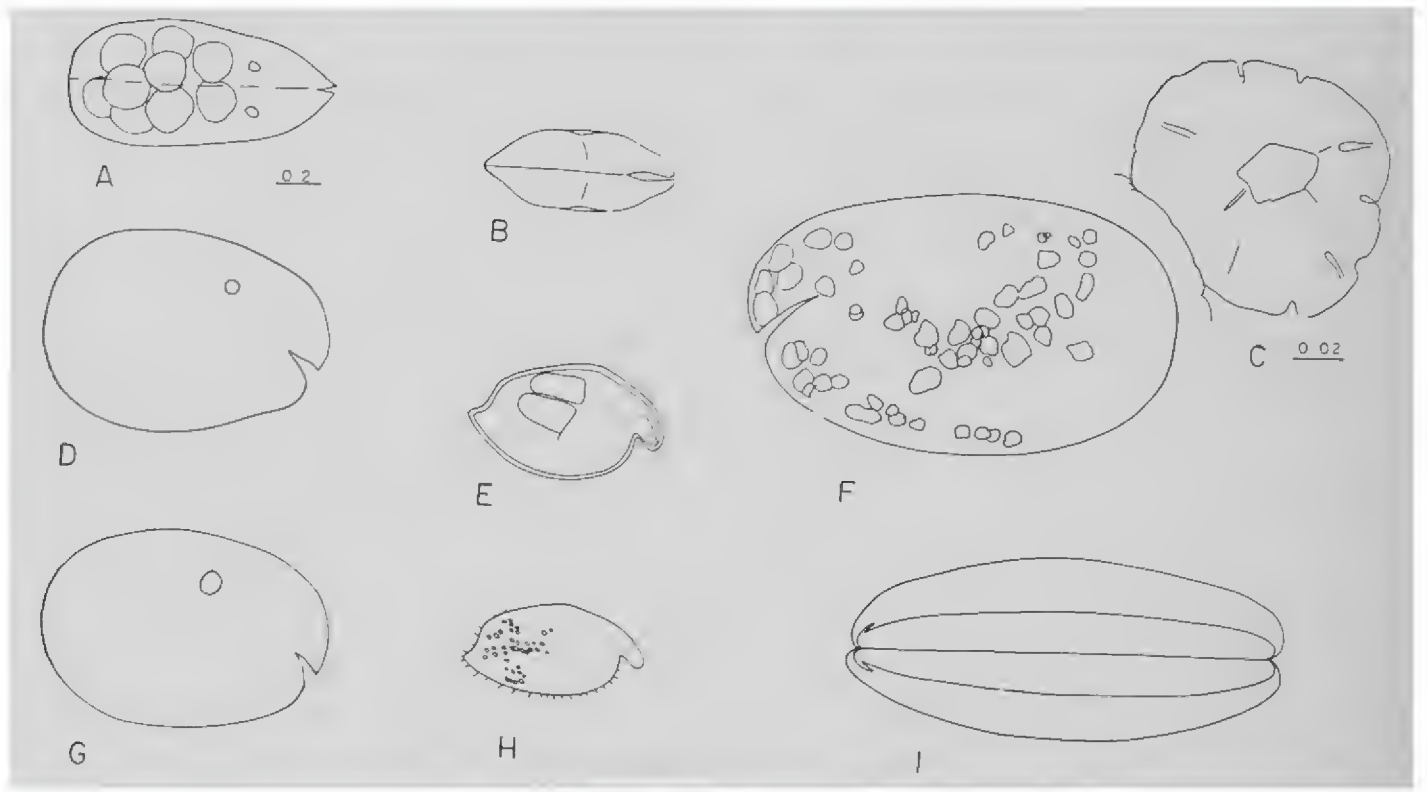

FIG. 87.

A, D, G. *Asteropina mulleri* (Skogsberg), female. A, Dorsal view showing eggs; D, Side view. Specimen No. CP5–1. G, Side view. Specimen No. CP5–3.

B, E, H. *Philomedies paucichelata* Kornicker, new species, female. B, Dorsal view; E, Side view (outlined areas on shell are slight depressions). Specimen No. 288–1. H, Side view. Specimen No. 156–7.

F, I, C. *Asteropina extrachelata* Kornicker, new species, female. F, Side view (internal occurred after death); I, Ventral view with valves slightly parted; C, Detail of an internal mark. Specimen No. 118–1. Figures with similar magnification, A, B, D-I; C.

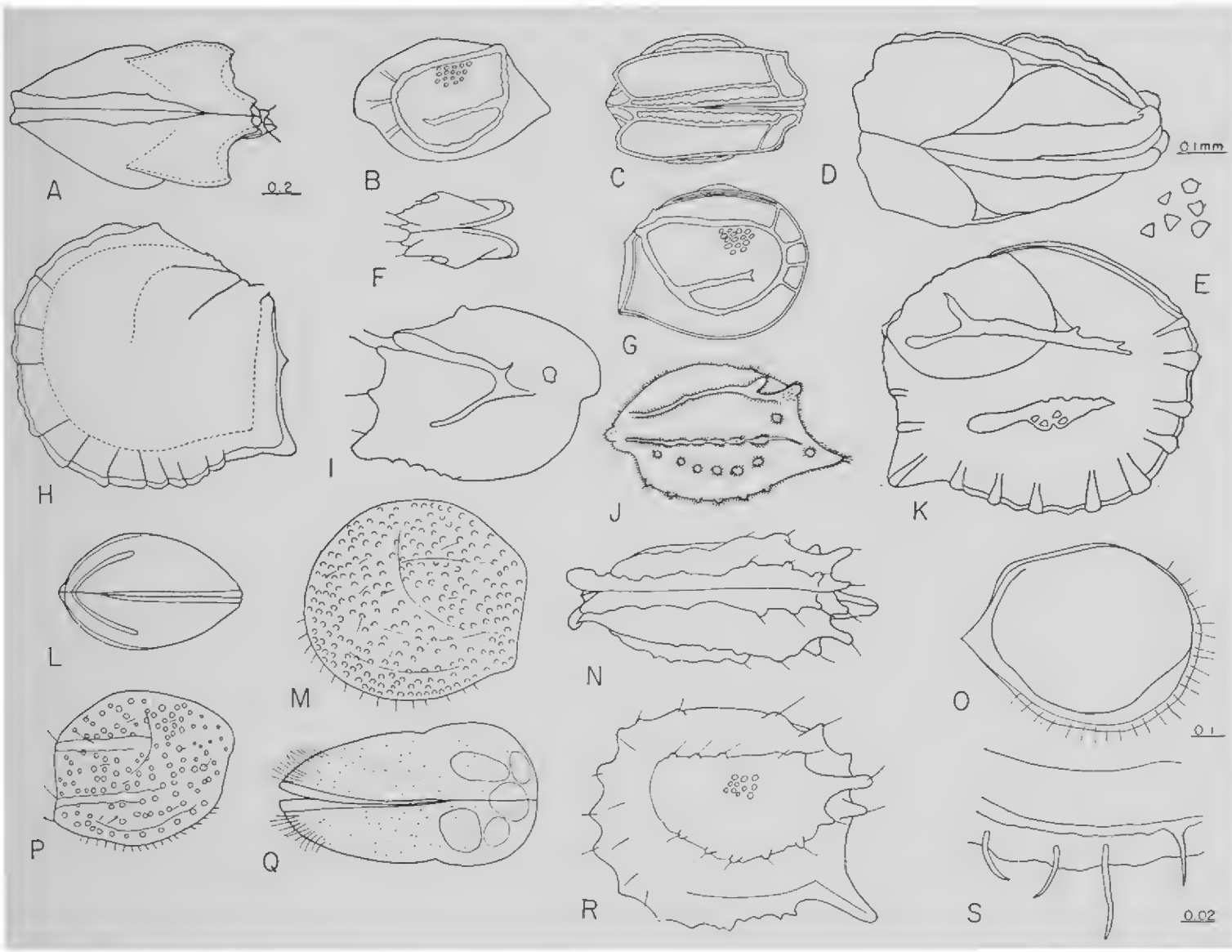

FIG. 88.

A, F, H, I. *Sarsiella gigacantha* Kornicker, new species. A, Dorsal view; H, Side view. Specimen No. 190–1A (female). F, Dorsal view with valves partly open (sketch); I, Side view. Specimen No. 122D–2 (male).

B, C, G. *Sarsiella costata* Kornicker, new species. B, Side view. Specimen No. CP52–7 (male). C, Dorsal view; G, Side view. Specimen No. 156–2 (female).

D, K, E, O, S. *Sarsiella sculpta* Brady. D, Dorsal view slightly tilted; K, Side view; E, Detail of surface pits. Specimen No. 127–1 (female). O, Inside view of left valve; S. Detail of antero-ventral edge. Specimen No. CP38–8 (female).

L, M, P. *Sarsiella punctata* Kornicker, new species, male. L, Dorsal view; P, Side view. Specimen No. 119A–1 (male). M, Side view. Specimen No. CP38–9 (female).

J, N, R. *Sarsiella carinata* A. Scott, male. J, Side view. Specimen No. CP52–23 (Male). N, Dorsal view; R, Side view. Specimen No. 686X–2.

Q. *Sarsiella truncana* Kornicker, new species. Q, Dorsal view showing internal eggs. Specimen No. CP52–21 (female). Figures with similar magnification, A-D, H-N, P-R; E; O; S.

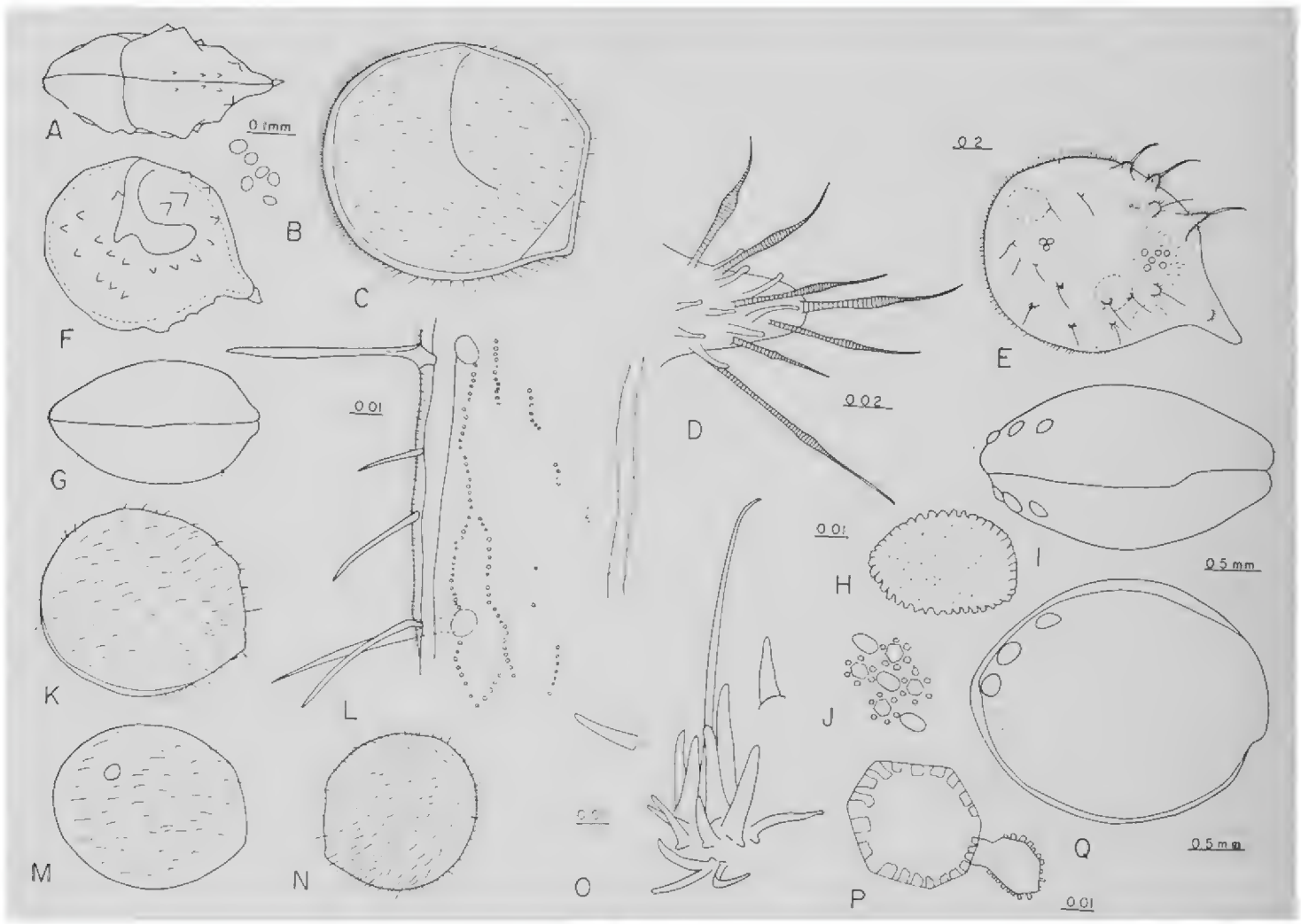

Fig. 89.

A, B, D, F, O. *Sarsiella capillaris* Kornicker, new species, female. A, Dorsal view; F, Side view; B, Detail of surface pits. Specimen No. 92–1. D, Shell hairs on posterior end of shell; O, Arrangement of clump of hairs on shell. Specimen No. CP38–10.

E. *Sarsiella carinata* A. Scott, female of immature instar. E, Side view. Specimen No. CP38–5.

C. *Sarsiella truncana* Kornicker, new species, female.C, Side view. Specimen No. CP52–21.

G, K-N. *Chelicopia arostrata* Kornicker, new genus, new species. G, Dorsal view; K, Side view. Specimen No. 91–1. L, Inside view of detail of anterior edge (female). Specimen No. CP38–16. M, Side view (eye is bright orange). Specimen No. 118A–1. N, Side view. Specimen No. CP38–16.

H-J, P, Q. *Actinoseta chelisparsa* Kornicker, new species. I, Dorsal view; Q, Side view. Specimen No. CP38–2. J, Surface pits; H, P. Detail of surface pits. Specimen No. C–1. Figures with similar magnification, A, C, F, G, K, M, N; B; D; E; H, L, O, P; I, Q; J.

Trematode Parasites of *Donax variabilis* at Mustang Island, Texas

SEWELL H. HOPKINS

The A. and M. College of Texas, College Station

Introduction

In 1951 and 1952. Harold C. Loesch[1] carried out an ecological study of the populations of coquina clams. *Donax variabilis* Say and *Donax tumida* Philippi. on the Gulf beach of Mustang Island. Loesch (1957) included in his ecological report some data on parasites of *Donax*. with illustrations of certain species. but did not name any of them. The purpose of the present paper is to name the trematodes found in *Donax variabilis* at Mustang Island. to describe them so they can be identified by other workers. and to discuss their biological significance. The author studied the parasites of *Donax* with Loesch in 1951 and 1952. and made a more intensive study of some of them in June. 1957. while employed on the summer staff of the Institute of Marine Science.

Most of the parasites previously known from *Donax* have been described by European workers. mainly from the coast of France. The European species include a bucephalid cercaria identified by Giard (1897a) as *Bucephalus haimeanus* Lacaze-Duthiers, 1854. metacercariae of *Gymnophallus* sp., and two trichocercous cercariae, *Cercaria pectinata* Huet, 1891 and *C. lutea* van Beneden. 1870, of Giard, 1897a. There is considerable literature on each of these species. The author has the opinion that Giard's bucephalid was not *B. haimeanus* but a still unnamed species distinct from the one found by Lacaze-Duthiers in *Ostrea edulis*. Rees (1939) believed the gymnophallids found in *Donax* to be metacercariae of the tailless *Cercaria strigata* Lebour, 1908. from sporocysts in *Cardium edule*, and thought that the adult form was some *Gymnophallus* of birds. most likely *G. deliciosus* (Olsson) of gulls. Palombi (1934) reported that *Cercaria pectinata* (or a similar trichocercous cercaria) encysted in amphipods and developed into adults of the fellodistomatine species *Bacciger bacciger* (Rudophi) in fishes which ate the amphipods. Dollfus (1946) considered the *Cercaria lutea* van Beneden of Giard to be a synonym of *C. pectinata* Huet. This species (if it is only one) has been reported from *Donax vittatus* Da Costa (*D. anatinus* Lamarck) as well as from *D. trunculus* L.

The only American trematode reported from *Donax* prior to the publication of Loesch (1957) is the monorchiid *Postmonorchis donacis* Young, 1953, whose sporocysts, cercariae. and metacercariae are found in *D. gouldii* Dall on the coast of southern California. The life cycle of this species was described by Young (1953).

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[1] Mr. Loesch was a graduate student in biological oceanography under Dr. J. G. Mackin at the A. and M. College of Texas. His study was guided by Mr. M. D. Burkenroad and Dr. Gordon Gunter of the Institute of Marine Science at Port Aransas on Mustang Island.

Descriptions of Species

Parvatrema donacis n. sp.

Cable (1953) described the adult, metacercaria, and cercaria of a new gymnophalline, *Parvatrema borinqueñae*, from Puerto Rico. The new genus *Parvatrema* was said to differ from *Gymnophallus* Odhner, 1900, by having a large pit-like genital pore anterior to the ventral sucker, a short genital atrium, a well-developed pharynx, only one group of vitelline follicles, and the excretory formula 2 [(2 + 2) + (2)]. Metacercariae of *Parvatrema borinqueñae* were found in the snail *Cerithidea costata*, and sporocysts and cercariae in the small clam *Gemma purpurea*. Cable obtained adults five days after feeding metacercariae to baby chicks, and guessed that the natural final host might be a wild duck.

Metacercariae of the gymnophalline type, found in at least 85 per cent of the *Donax variabilis* on Mustang Island beach, have the features listed by Cable as distinctive for the genus *Parvatrema* but differ from *P. borinqueñae* in some morphological details as well as in host and locality. They are therefore considered to represent a new species, *P. donacis*. All metacercariae from *Donax variabilis* have lateral diverticula of the excretory bladder, posterior to the testes, which are not mentioned or illustrated by Cable. These and other structures are shown in Figure 1. Lateral papillae on the oral sucker,

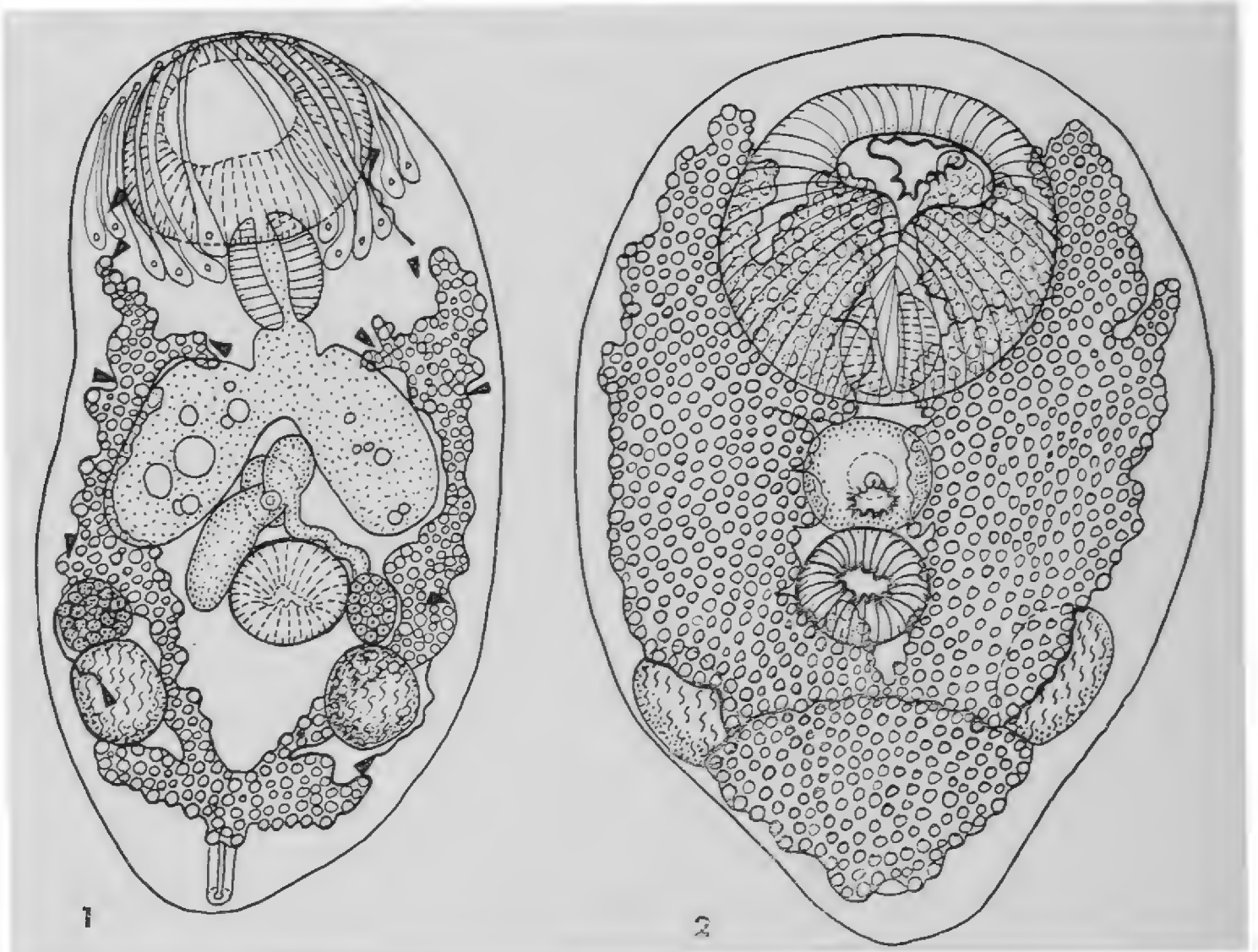

FIG. 1. *Parvatrema donacis* metacercaria, living, dorsal view, drawn with camera lucida. Length 0.29 and width 0.15 mm. Note lateral diverticula of excretory bladder posterior to testes, ovary anterior to right testis, and vitellarium, anterior to left testis.

FIG. 2. *Parvatrema donacis*, older metacercaria with expanded excretory bladder, living, ventral view, drawn with camera lucida. Length 0.30 and width 0.21 mm. Note common genital pore anterior to ventral sucker.

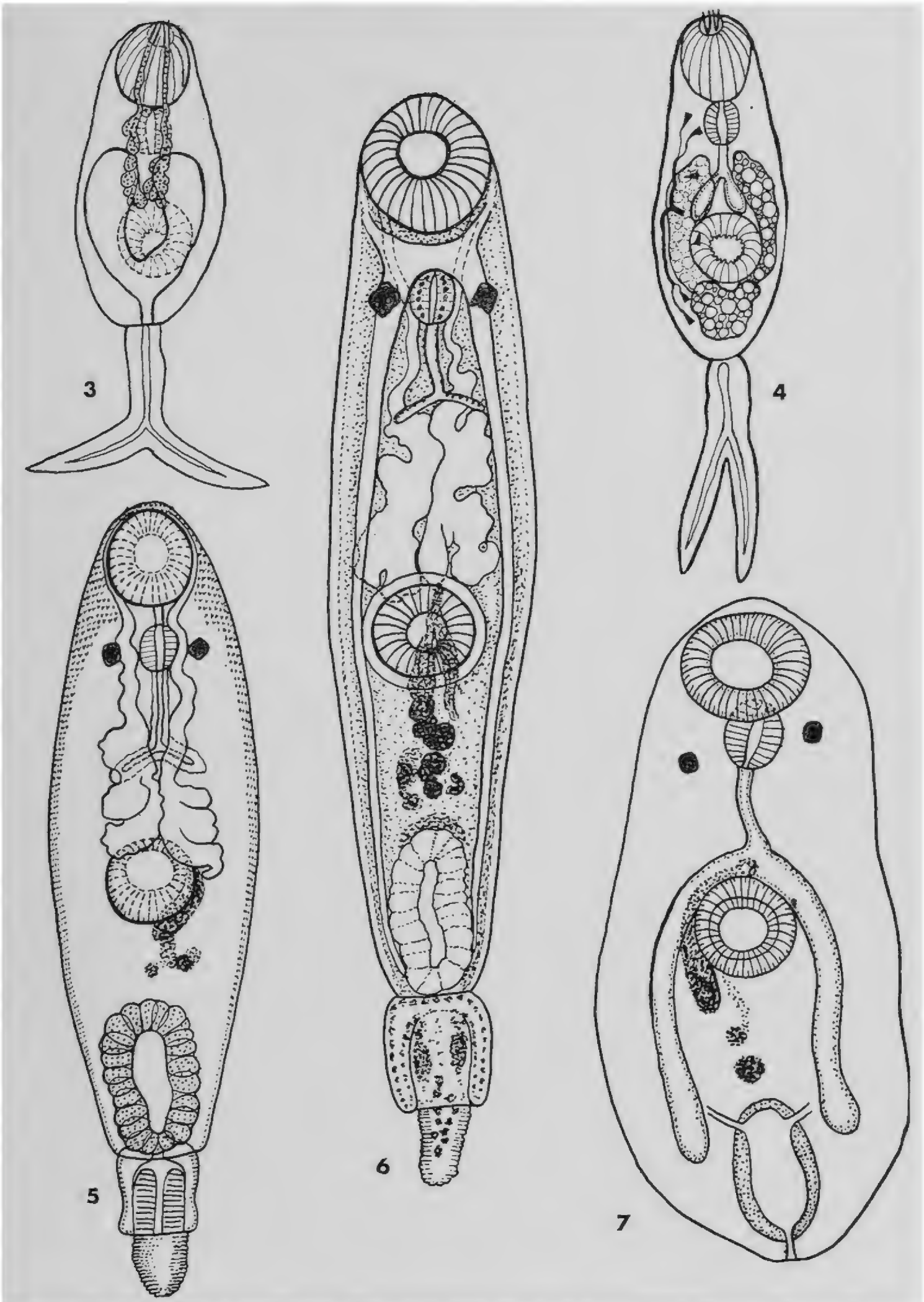

FIG. 3. Cercaria of "dichotoma" type, believed to be *Parvatrema donacis* cercaria, from sporocyst in *Donax variabilis*, alive, dorsal view, drawn with camera lucida.

FIG. 4. Cercaria believed to be *Parvatrema donacis* cercaria, alive, ventral view, drawn with camera lucida.

FIG. 5. *Cercaria choanura* from sporocyst in *Donax variabilis*, alive, slightly flattened, stained with neutral red; dorsal view, drawn with camera lucida. Length 0.28 and width 0.09 mm.

FIG. 6. *Cercaria choanura*, killed in formalin and stained with alum cochineal; ventral view, drawn with camera lucida. Length 0.275, width 0.063 mm.

FIG. 7. Metacercaria dissected from cyst in *Donax variabilis*, believed to be the metacercarial stage of *Cercaria choanura*, alive, stained with neutral red; ventral view, drawn with camera lucida (composite of several specimens).

like those of *P. borinqueñae*, were seen on some specimens. Cephalic glands could not be counted accurately, even when stained with neutral red. Twelve flame cells, placed exactly as in Cable's Figure 1, were observed and drawn before Cable's drawings were seen. Connections of all tubules were not traced, but there seems to be no reason to doubt that *P. donacis* has the same excretory formula as *P. borinqueñae*, 2 [(2 + 2) + (2)]. Young, active metacercariae (Fig. 1) average 0.33 mm. in length and 0.17 mm. in width, with the oral sucker averaging 0.090 by 0.086 mm., the ventral sucker 0.037 by 0.039 mm., and the pharynx 0.036 by 0.030 mm. Older metacercariae (Fig. 2), up to 0.80 mm. long and 0.50 mm. wide, are nearly motionless and so full of excretory concretions and other minute spherical bodies (parasites?) that they are quite opaque. Many of these older metacercariae eventually become calcified and sealed into the inner lining of the shell not far below the hinge, as has been reported for the metacercariae of *Gymnophallus* in Europe. Like other gymnophallines, the metacercariae of *P. donacis* remain unencysted but are surrounded by a zone of liquid or semi-liquid secretions.

A furcocercous cercaria of the "dichotoma" type was found in eight of the 1017 *Donax variabilis* examined by Loesch in 1951 and 1952, but was not found in any of the 100 clams dissected by the author in 1957. All of the known cercariae of this type, named for *Cercaria dichotoma* Mueller, 1855, develop from sporocysts in marine bivalves. Markowski (1936), partly on the basis of a clue furnished by Pelseneer (1906), suggested that "dichotoma" cercariae are larvae of gymnophallines. Loesch (1957) called the metacercariae of *P. donacis* "*Gymnophallus* metacercariae" because of their resemblance to the European species assigned to that genus, and called the "dichotoma" cercariae "*Gymnophallus* cercariae" because of Markowski's theory, the close association of cercaria and metacercaria in Mustang Island *Donax*, and the absence of any other cercaria which might be a gymnophalline. The cercaria of *P. borinqueñae* Cable, described in 1953, is so similar to the one found in *Donax variabilis* that it now seems virtually certain that the latter is the cercaria of *P. donacis*.

The *Donax* cercaria (Figs. 3 and 4) is somewhat larger than the Puerto Rican cercaria from *Gemma*, live specimens averaging 0.132 mm. in length and 0.058 mm. in width, with a range of 0.120 to 0.145 mm. in length and 0.050 to 0.065 mm. in width. The oral sucker averages 0.036 by 0.032 mm., the ventral sucker 0.033 by 0.032 mm., and the pharynx 0.017 by 0.016 mm. The tail is 0.044 mm. from body to fork, and 0.050 mm. from fork to tips of furci. No papillae were noted, and no setae, either on the body or on the tail. Cephalic glands are so inconspicuous that they could not be counted accurately. Flame cells and excretory tubules are exactly as in *P. borinqueñae*, but the connection of the tubule from the second pair of flame cells could not be seen, and excretory openings in tail furci, if present, were not noticed. These cercariae develop in short sporocysts, 0.40 to 0.60 mm. long and 0.14 mm. wide, in the gonad of *Donax variabilis*. Each sporocyst bears approximately six cercariae. The gonads of the eight infected clams contained no gametes.

Parvatrema and *Gymnophallus* are fellodistomatids of the subfamily Gymnophallinae which have their adult forms in the intestines of birds. Cable (1953) obtained adults of *Parvatrema borinqueñae* experimentally in baby chicks, and thought wild ducks might be the natural final hosts. Wild ducks do not feed on the Mustang Island beach. The final host of *P. donacis* is probably some wading bird or shore bird. Loesch (1957) observed black-bellied plovers, sanderlings, and Eastern willets feeding on *Donax*, but did not find trematodes in the few individuals he examined. The author fed metacercariae

of *P. donacis* to two one-week-old chicks in July, 1957, but failed to find any trematodes when the intestines were examined under a binocular dissecting microscope five days later. It is possible that younger chicks would have given positive results.

Cercaria choanura n. sp.

This very distinctive cercaria was found in 26 of the 1017 *Donax variabilis* examined by Loesch in 1951–1952 and in one of the 100 examined by the author in 1957. It comes from orange-pigmented sporocysts 1.5 to 2.0 mm. long and 0.4 to 0.5 mm. wide which develop in the gonad and cause parasitic castration of the host. The stubby, transversely striated or "corrugated" tail of the cercaria is held by a muscular collar-like base, into which the tail can be withdrawn when the cercaria is crawling. This unique structure suggested the name "choanura." No other cercaria known to the author has a tail of this type. In dilute neutral red solution, the tail proper stains red but the collar remains unstained.

Cercaria choanura is shown in Figures 5 and 6. Rows of minute spines or scales circling the body give it a transversely striated appearance. There are no specialized penetration spines. Cephalic glands, apparently three pairs, lie just anterior to the ventral sucker. They stain red in diluted neutral red. Ducts from the glands open dorsally near the anterior tip of the body. There is an anteroventral mouth, a nearly round oral sucker, a short prepharynx, a small but distinct muscular pharynx, and a narrow esophagus which runs to a point halfway between the two suckers and there divides into two short, indistinct ceca. In stained specimens genital analagen can be seen, apparently anlagen of gonads just anterior to the excretory bladder and of ducts running anteriad over the dorsal side of the ventral sucker. The conspicuously granular cells of the thick bladder wall are reddish-brown in live cercariae stained with neutral red, and brown in formalin-fixed specimens stained with alum cochineal. No excretory tubes or flame cells were seen in the short time available for study of live cercariae. Nerve cords and ganglia (unstained) were seen in some cochineal-stained specimens (Fig. 6). Living, unflattened cercariae and specimens killed in cold formalin had approximately the same average measurements: Length of body 0.280 mm., width 0.080 mm., oral sucker 0.044 by 0.038 mm., ventral sucker 0.036 by 0.037 mm., pharynx 0.020 by 0.015 mm., tail collar 0.042 by 0.037 mm., and tail proper 0.024 mm. long beyond the collar.

Cercaria choanura is the "Cercaria A" of Loesch (1957). Cable in private correspondence expressed the opinion that this cercaria belongs to the family Monorchiidae, the adult forms of which live in the intestine of fishes. The author agrees, although *C. choanura* is very different from the cercariae assigned to *Monorcheides cumingiae* by Martin (1938, 1940) and to *Postmonorchis donacis* by Young (1953). Both of those cercariae have tails nearly as long as the body, covered with circular rows of prominent scales, and do not have a collar-like tail base. The cercaria of *M. cumingiae* develops in sporocysts in the visceral mass of the marine clam *Cumingia tellinoides* in Massachusetts. Metacercariae, in the same clam or in *Tellina tenera,* developed into adults within four weeks after they were fed to eels and flounders. The cercaria of *Postmonorchis donacis* develops from sporocysts in *Donax gouldii* on California beaches and encysts in the same clam. Encysted metacercariae fed to Embiotocidae (surf perches) developed into adults. Both Martin and Young compared their cercariae with the European *Cercaria myocerca* Villot, 1878, from the marine clam *Scrobicularia tenuis.*

Loesch and the author found encysted metacercariae apparently belonging to *Cercaria choanura* in both *Donax variabilis* and *D. tumida* at Mustang Island, and in *Donax tumida* at Grand Isle, Louisiana, where *D. variabilis* does not occur. These metacercariae were most abundant in the walls of the incurrent siphon and in nearby parts of the mantle. They were seen in 72 of the 100 *Donax variabilis* dissected at Mustang Island in June, 1957, and in all of the relatively small number of *D. tumida* examined at Grand Isle. One *Donax* from Grand Isle, examined by Loesch, contained sporocysts and *Cercaria choanura*. No other trematode larvae were found on the Grand Isle beach. The metacercaria (Fig. 7) believed to be an advanced stage of *C. choanura* is coiled within a cyst usually 0.125 to 0.150 mm. in diameter, rarely as much as 0.250 mm. Pigmented eyespots, suckers, pharynx, and excretory bladder are clearly visible through the thin cyst wall. Dilute neutral red stains the esophagus and intestine a conspicuous red. Only a few metacercariae were dissected intact from cysts, after many attempts. Two intact live specimens measured 0.25 and 0.28 mm. long, 0.12 and 0.13 mm. wide, with oral suckers 0.047–0.050 by 0.056–0.060 mm., ventral suckers 0.043 by 0.045 mm., and pharynx 0.030 by 0.025 mm. No cephalic glands were seen, even in neutral red solution. The pharynx was larger and the intestinal ceca were longer than in the cercaria. Flame cells and excretory tubules were not seen during the short time living metacercariae were studied. Figure 7 shows one of these metacercariae.

Bucephalus loeschi n. sp.

Three of the 1017 *Donax variabilis* examined by Loesch in 1951–1952 and two of the 100 examined by the author in 1957 contained sporocysts and cercariae of a bucephalid. This species was mentioned by Hopkins (1951) and Loesch (1957) but was not described. It seems best to name and describe it now even though some details of its morphology remain uncertain. The principal characteristics of the *Donax* bucephalid are shown in Figures 8 and 9. The species is named for its discoverer, Harold C. Loesch, and placed provisionally in the genus *Bucephalus* von Baer, 1827. This is the type genus of the family Bucephalidae, and the name was first used for *B. polymorphus*, the first-known bucephalid cercaria.

Bucephalus loeschi closely resembles *B. cuculus* McCrady as redescribed by Hopkins (1954). It tends to be more elongate than the latter in life, being sometimes ten times longer than wide. The pharynx is farther back, in the last fifth of the body length in elongated individuals and seven-tenths of the way back in contracted cercariae. The excretory bladder is shorter than in *B. cuculus*, extending little more than halfway from the posterior end to the level of the pharynx. Five living cercariae had the following average measurements: Body length 0.382 mm., width 0.049 mm.; pharynx four-fifths of the distance from anterior to posterior end; anterior "sucker" 0.059 by 0.030 mm., pharynx 0.027 by 0.028 mm., tail stem 0.063 mm. long and 0.085 mm. wide, tail furci 0.016 mm. wide and up to 2.25 mm. long. Measurements of five formalin-killed specimens averaged as follows: Body length 0.254 mm., width 0.060 mm.; pharynx seven-tenths of distance from anterior to posterior end; anterior "sucker" 0.037 by 0.030 mm., pharynx 0.015 by 0.021 mm., tail stem 0.048 by 0.093 mm., tail furci 0.022 mm. wide and 0.60 to 0.65 mm. long. The longest living cercaria was 0.440 mm. long and 0.043 mm. wide, and the shortest formalin-killed specimen was 0.217 by 0.063 mm.

Figures 8 and 9 give only an approximation or impression of the gland cells around the anterior "sucker" and pharynx, for these were never seen very distinctly. Genital

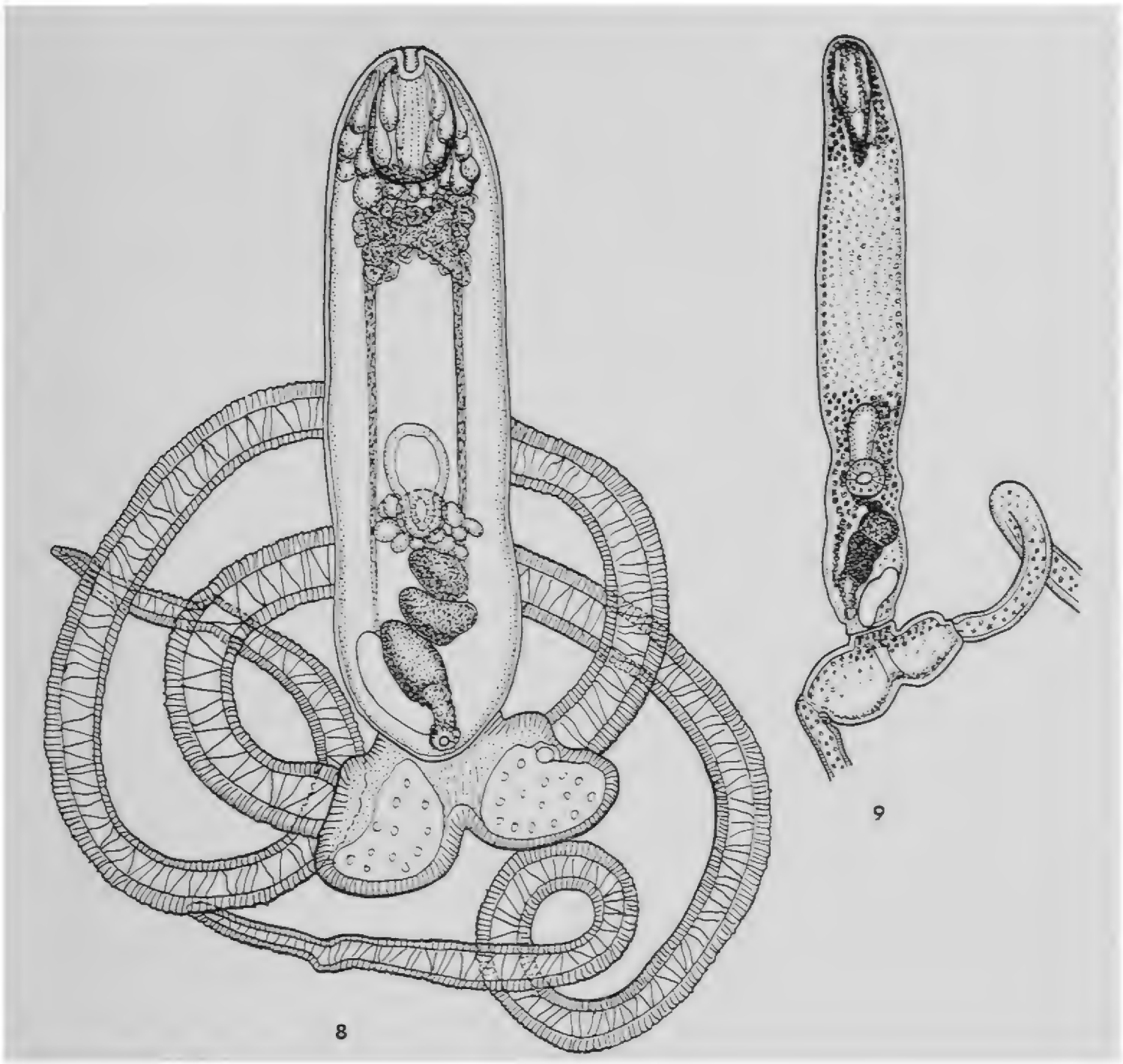

FIG. 8. *Bucephalus loeschi*, cercaria from sporocyst in *Donax variabilis*, alive and slightly flattened, stained with neutral red; dorsal view, drawn with camera lucida. Length of body 0.23 and width 0.06 mm.

FIG. 9. *Bucephalus loeschi*, balsam mount, stained with alum cochineal, ventral view, drawn with camera lucida.

anlagen, though conspicuous in all specimens, were not consistent in form and arrangement. It is suspected that all cercariae seen were somewhat immature; naturally emerged cercariae might show structural details more distinctly. Sporocysts of *B. loeschi* are long and branched like those of other bucephalids. All of those seen were in the gonadal region, where they replaced germinal tissues and caused parasitic castration of the host. Spots of orange pigment in sporocysts give the infected gonad a yellow color, as seen with the naked eye.

Bucephalid cercariae identified as *Bucephalopsis haimeanus* have been reported from *Donax trunculus* in Europe by Giard (1897a) and others. The author doubts that the cercaria from *Donax* is the same as the one from the European oyster, *Ostrea edulis*. *Cercaria caribbea* XLII, a new bucephalid cercaria found in *Donax denticulata* in Puerto Rico by Cable (1956), differs from the Mustang Island species by its smaller size, more slender tail, longer excretory bladder, and some differences in minor features.

Adult bucephalids known from Mustang Island and vicinity include *Rhipidocotyle*

transversale, *R. lintoni*, and *Bucephaloides strongylurae*, all from the needle gar, *Strongylura marina*. The cercariae of these species are unknown. *Bucephalus cuculus* cercariae, known to occur in Aransas Bay oysters, *Crassostrea virginica*, probably develop into *Rhipidocotyle lepisostei* in alligator gars, *Lepisosteus spatula*, but this has not been proved experimentally. An unidentified bucephalid cercaria was found once in the Gulf oyster, *Ostrea equestris*, at Port Aransas. Further search would probably reveal the presence of many other bucephalids, larval and adult, in this little-studied region.

Lobatostoma sp.

An immature aspidogastrid belonging to the genus *Lobatostoma* Eckmann was found in a *Donax variabilis* by Loesch in the summer of 1951. No additional specimens were found in the 1017 clams dissected by Loesch, nor in those examined by the author. Adults of this genus live in intestines of marine fishes, including pompanos and croakers.

Discussion

The trematodes now known from *Donax* in America belong to the three families Monorchiidae *(Postmonorchis donacis* and presumably *Cercaria choanura)*, Bucephalidae *(Cercaria caribbea* XLII and *Bucephalus loeschi)*, and Fellodistomatidae *(Parvatrema donacis)*. The known European species belong to the last two of these families. The subfamilies Gymnophallinae, represented by *Gymnophallus* and *Parvatrema*, and Fellodistomatinae, represented by *Bacciger*, were placed together in the family Fellodistomatidae by Cable (1953). All of the known American parasites of *Donax* are different from any known European species.

Pelseneer (1896, 1928) blamed heavy infections of *Cercaria pectinata* for periodic "decimations" of *Donax vittatus* on the northern coast of France. Jobert (1894) attributed an abnormal mortality of *Tapes decussata* and *T. pullastra* at Arcachon to a high incidence of a trichocercous cercaria similar to *C. pectinata*. Coe (1946) mentioned "trematode parasites," probably sporocysts and cercariae of *Postmonorchis donacis*, as one of the agents controlling California populations of *Donax gouldii*. Later, Coe (1955) attributed "epidemic disease" of *Donax gouldii* to a unicellular parasite 2–6 μ in diameter, which he compared to the oyster parasite *Dermocystidium marinum*. In Europe the coccidian *Hyaloklossia pelseneeri* Leger, which has spherical oocysts 75 to 80 μ in diameter, has been reported from the kidney of *Donax*.

Most, if not all, of the known trematode parasites of pelecypods have been reported to cause parasitic castration of the hosts. Parasitic castration of *Donax* was reported for "*Bucephalus haimeanus*" and "*Cercaria lutea*" by Giard (1897a), for *Cercaria pectinata* by Pelseneer (1896, 1928) and others, and for *Postmonorchis donacis* by Young (1953). Loesch and the author found that *Donax variabilis* was made sterile by the sporocysts of *Cercaria choanura*, *Bucephalus loeschi*, and the "dichotoma" cercaria which we believe belongs to *Parvatrema donacis*.

Metacercariae probably do not kill or sterilize *Donax*. However, it is probable that heavy infections affect the growth of this small clam, in view of the adverse effects on the much larger *Crassostrea gigas* that Hoshina and Ogino (1952) found to be caused by metacercariae of *Gymnophalloides tokiensis* Fujita, 1925.

Hyperparasitism of sporocysts of *Cercaria pectinata* in *Donax vittatus* by the "haplosporidian" *Anurosporidium pelseneeri* Caullery and Chapellier, 1906, was first re-

ported from the northern French coast by Pelseneer (1896), although he did not recognize the nature of the protistan parasites. Cepédè (1911) made a careful study of the hyperparasite. Dollfus (1925, 1946) restudied it and found the original description in error, so he placed *A. pelseneeri* in the genus *Urosporidium* Caullery and Mesnil, 1905. *Urosporidium pelseneeri* and a similar species (described by Guyénot, 1943) infecting sporocysts in *Barnea candida* cause "parasitic castration" of the trematode; that is, infected sporocysts fail to produce cercariae and become filled with hyperparasites instead.

Nosema legeri Dollfus, 1912, a microsporidian hyperparasite of *Gymnophallus* metacercariae in species of *Donax* from France was reported by Giard (1897b) and Leger (1897), and was later studied by Jameson (1902), Guyénot, Naville and Ponse (1925), Dollfus (1912, 1946), and others. According to Dollfus, the *Nosema* infection gradually kills the metacercariae; as these become moribund, the mantle of the clam seals them over with calcareous deposits. Similarly, *Parvatrema donacis* metacercariae are sealed into the shell lining after they become large, inactive, opaque, and packed with minute round bodies of unknown nature. Dr. J. G. Mackin once examined these minute bodies and was not convinced that they were parasites, but he did not have time to make a thorough study.

An interesting sidelight is the relationship of the *Donax* parasites to the parasites which supposedly cause pearl formation in larger bivalves. Giard (1897b) found pearls formed around *Gymnophallus* metacercariae in several species of *Tellina*, and possibly in *Donax*. Dubois (1901) claimed that metacercariae of *Gymnophallus margaritarum*, but only those killed by sporozoan infections, became the nuclei of fine pearls in *Mytilus edulis*. Dubois (1907, 1909) found sporozoan spores in the nuclei of pearls in *Margaritifera vulgaris*, *Modiola barbata*, and *Pinna nobilis* on the Tunisian coast and suspected that the pearls were formed around the cysts of trematode and cestode larvae killed by hyperparasites. Dollfus (1946) said the parasitic worms were probably killed by a *Nosema*, similar to the species he found killing *Gymnophallus* metacercariae in *Donax vittatus*. Dubois (1903) claimed to have increased enormously the pearl production of Tunisian pearl oysters, *Margaritifera vulgaris*, by transplanting them to waters where mussels, *Mytilus galloprovincialis*, were heavily infected by *Gymnophallus duboisi* metacercariae containing hyperparasitic sporozoans.

Summary

Sporocysts and cercariae of three species and metacercariae of two species occur in coquina clams, *Donax variabilis* Say, on the Gulf beach of Mustang Island at Port Aransas, Texas. In addition, an immature aspidogastrid, *Lobatostoma* sp., was found once. The cercariae are *Bucephalus loeschi*, *Cercaria choanura*, and a "dichotoma" cercaria. The bucephalid presumably penetrates and encysts in some fish and becomes adult in a second fish that eats the first one. *Cercaria choanura* is presumed to develop into a metacercaria which is found encysted in most of the *Donax* of Mustang Island, and to become an adult monorchiid in some fish that eats coquina clams. *Cercaria choanura* and the metacercaria presumed to develop from it also were found in *Donax tumida* at Grand Isle, Louisiana and at Mustang Island. A gymnophalline metacercaria described as *Parvatrema donacis*, presumed to develop from the "dichotoma" cercaria, is found in most of the Mustang Island *Donax;* it probably becomes adult in some clam-eating shore

bird. All of these digenetic trematodes are considered to be new species. Previously known parasites of *Donax* are discussed. Parasitic castration is caused by all known sporocysts in *Donax*.

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A Partially Annotated Checklist of the Marine Fishes of Texas[1]

HINTON D. HOESE[2]

Department of Biology, A. & M. College of Texas, College Station, Texas
and
Marine Laboratory, Texas Game and Fish Commission, Rockport, Texas

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Introduction

This paper is basically the result of a literature survey with the attempt to list all the species of fishes known to occur in Texas marine waters. The annotations are not intended to be complete, except for rare or uncommon forms, but are included for the use of the interested student for further study and the establishment of a species presence in Texas waters. Doubtful records are not included in the systematic listing but are mentioned in a discussion under the proper category.

As many species as possible were examined from the collections of the Institute of Marine Science of the University of Texas at Port Aransas, the Department of Wildlife Management of the A. and M. College of Texas at College Station, and the Marine Laboratory of the Texas Game and Fish Commission at Rockport. References to specimens in these collections are abbreviated in the annotations as follows: IMS (Institute of Marine Science), ML (Marine Laboratory), AM (A. and M. College). Other abbreviations include CNHM (Chicago Natural History Museum), FWS (Fort Crockett Laboratory, Fish and Wildlife Service, Galveston), USNM (U.S. National Museum).

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[1] Contribution No. 42 of the Marine Laboratory, Texas Game and Fish Commission, Rockport, Texas.
[2] Present address. Field Laboratory, Texas Game and Fish Commission, Seabrook, Texas.

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Previous Works on Texas Marine Fishes

Even though the ichthyofauna of Texas has received more attention than any other Gulf state, excepting possibly Florida, present workers have little idea of the number of species and their distribution along the Texas coast. Baughman (1950a, 1950b) has compiled the only extensive list, including both marine and freshwater fishes. This list, even though incomplete and perpetuating many errors, compiles a great deal of scattered information. Since that time many taxonomic revisions have helped clarify the status of many of our marine fishes. The most important of these are Ginsburg (1950, 1951a 1951b, 1952b, 1952c, 1954), Rivas (1950, 1951), and Briggs (1955).

The literature cited includes the main systematic and ecological studies that have bearing on Texas marine fishes. Most of the older references are not included. Baughman (1950b) lists a fairly complete number of these.

Zoogeographic Considerations

The status of Texas marine fishes from the standpoint of Gulf zoogeography is not completely clear, but some progress is being made in this field. Baughman (1950a) believed that the western Gulf was a separate entity from the eastern Gulf, divided by the silt laden flood of the Mississippi. Ginsburg (1952a) generally supports this theory with a different line of division, based on the distribution of four species. He speculates on an east-west faunal break from two viewpoints: First, the division of populations at the species level exemplified by *Archosargus probatocephalus* and *Hippocampus zosterae*, two eastern Gulf species, and their counterparts *A. oviceps* and *H. regulus* in the western Gulf; second, the presence of two new species on the western Florida coast not known from the western Gulf. *Menticirrhus focaliger* and *Centropristes melanus*. Hildebrand (1955) subsequently questioned the value of the status of *A. oviceps* showing that the diagnostic characters of western Gulf *Archosargus* were noteworthy but not of species magnitude. Kirk Strawn (personal communication) likewise questions the status of *H. zosterae* and *H. regulus* and is presently revising the dwarf seahorses. Hildebrand (1954) also took *M. focaliger* from the Texas coast. *Centropristes melanus* has not been reported from Texas, although *C. striatus*, the Atlantic counterpart, was reported by Reed (1941). Even though Reed's (op. cit.) *Centropristes* were undoubtedly the common *philadelphicus*, *melanus* may occur in the western Gulf.

That there has been disagreement between authors as to a distinct qualitative faunal difference is clearly indicative as to the lack of information at this point. Several factors must be analyzed before any conclusions could be drawn.

The number of active marine ichthyologists in the northeastern Gulf outnumbers those in the northwestern. Recent additions to the known Texas fish fauna have most always been centered near the two marine laboratories on the Central coast. The more tropical region near Port Isabel has not been sampled intensively since the work of Evermann and Kendall (1894). As a result, the Texas fish fauna of this area is less well known.

For example Baughman (1950a, 1950b) lists near 200 species of marine fishes, whereas this list contains 424. Two studies in this area should produce significant contributions—those of the offshore reefs and "mud lumps," and of the jetties.

Briggs (1958) has listed 108 species from the northeastern Gulf, but unreported from the northwestern Gulf. Sixteen of these are reported in this list. He explains this apparent faunal difference by the coral sponge community present in that area but absent in the northwestern Gulf. While this difference is impressive, it still remains to be conclusively shown. Even the reef fishes, common in the southern Gulf, heretofore recorded from the Texas Coast, occur sporadically near oil rigs, jetties and banks, so even this difference may prove to be largely quantitative.

The recently reported species in this area have largely been the result of studies on the offshore and to a lesser extent pelagic fauna. Hildebrand's (1954) study, collections by the *Oregon* (Springer and Bullis, 1956) and collections by Mr. E. D. McRae, formerly of the Texas Game and Fish Commission, have added greatly to the knowledge of these fishes.

It seems likely that there is a much greater difference between the northern and southern Gulf of Mexico, the changes being gradual as noted by Reid (1954) for the west coast of Florida and Hildebrand (1954, 1955) for the east coast of Mexico. Many tropical species common in the southern Gulf are either absent in Texas waters or are apparently strays during warmer months.

Arrangement and Inclusion of Species

Fresh-water species are included on the basis of their known existence in bay waters over ten parts per thousand total salts. This is arbitrary, but should serve to eliminate many forms which lack the osmoregulatory mechanisms to maintain a marine population. The fresh-water fishes of the saltier Texas Rivers are not included, because it is felt that these are not a true part of the marine fauna.

For higher categories of bony fishes the writer has essentially followed Berg (1940). For the elasmobranchs, the classification of Bigelow and Schroeder (1948, 1953) has been used, except for the Carcharhinidae as modified by Springer (1950). For genera and species, the latest reviser of the group has been followed, where possible. In some cases the nomenclature is the writer's opinion, and here synonyms pertinent to Texas studies are included. Common names followed by an asterisk (*) are those accepted by the American Fisheries Society (see Chute, et. al., 1948 and supplements). Other common names used were chosen on the basis of widespread usage in this area.

Remarks on the abundance and distribution of the common forms are taken from the main ecological works on Texas marine fishes and from observations by the writer, and are not intended to summarize all information on a species.

For the purpose of this paper Texas waters are considered to be those which lie north

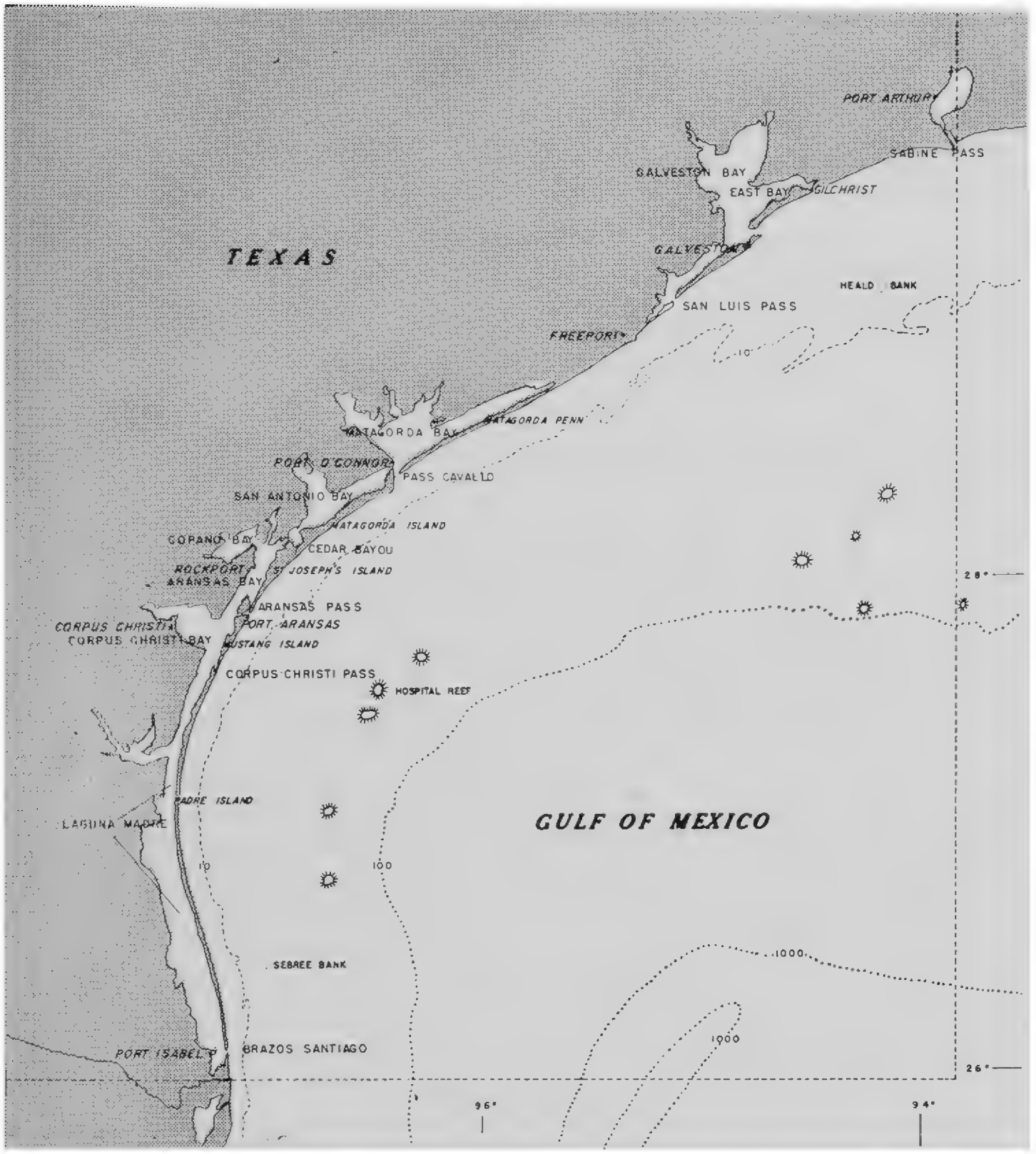

FIG. 1. Northwestern Gulf Waters. Those considered as Texas waters in this paper are inside dotted line. Reefs are marked with circles with radiating lines.

of 25° 58′ North Latitude and west of 93° 49′ West Longitude, including the bays and lagoons from the Rio Grande River to Sabine Lake (Fig. 1). This area includes waters outside of the 1000 fathom line. The fish fauna of these deeper waters is essentially uniform throughout the Gulf, but since these areas have been poorly collected, fishes known from this area are included.

Annotated List

BRANCHIOSTOMIDAE—Lancelets

Branchiostoma Costa

B. caribaeum Sundevall—Amphioxus. Lydia Ann Channel, (Baughman, 1950a); Port Aransas, (Gunter and Knapp, 1951); Aransas Bay flats off Mud Island, (ML), five specimens; Freeport, nine fathoms, (ML) three specimens.

ISURIDAE—Mackerel Sharks

Isurus Rafinesque

I. oxyrinchus Rafinesque—Mako* (Sharp-nosed Mackerel Shark). Port Isabel. (Baughman and Springer, 1950); off Port Aransas (Baughman, 1950a); snapper banks off Port Aransas (IMS).

Carcharodon Agassiz

C. carcharias (Linnaeus)—Great White Shark*. (Maneater). Near Port Aransas, (Baughman, 1950a); near Port Aransas, (Gunter and Knapp, 1951).

ALOPIIDAE—Thresher Sharks

Alopias Rafinesque

A. vulpinus (Bonnaterre)—Thresher Shark*. (Common Thresher). Near Port Aransas, (Gunter, 1941).

ORECTOLOBIDAE—Nurse Sharks

Ginglymostoma Müller and Henle

G. cirratum (Bonnaterre)—Nurse Shark.* Near Port Aransas, (Baughman, 1950a; Baughman and Springer, 1950). Port Aransas jetties, (IMS), jaw.

RHINCODONTIDAE—Whale Sharks

Rhincodon Smith

R. typus Smith—Whale Shark*. Near Port Isabel, (Baughman, 1947), sight record; off Port Aransas, (Baughman, 1950a), sight record; 18 miles southeast Port Aransas, (Gunter and Knapp, 1951), sight record. The embryo reported by Baughman (1955) and described by Reid (1957a) was taken off the coast of Mexico.

SCYLIORHINIDAE—Cat Sharks

Bigelow, et al., (1953) report *Apristurus atlanticus* (Koefoed) from near Texas waters and it should be expected here.

Scyliorhinus Blainville

S. retifer (Garman)—Chain Dogfish. Gulf, 220–260 fathoms, *Oregon* stations 541, 546, (Springer and Bullis, 1956).

TRIAKIDAE—Smooth Dogfishes

Mustelus Link

M. canis (Mitchell)—Atlantic Smooth Dogfish*. Off Port Aransas, (IMS). Hildebrand (1954) found this species abundant offshore.

CARCHARHINIDAE—Requiem Sharks

Baughman and Springer (1950) report *Prionace glauca* (Linnaeus) from doubtful sight records and *Eulamia springeri* (Bigelow and Schroeder) on the basis of geographic range. No specimens are known from the northwestern Gulf.

Galeocerdo Müller and Henle

G. cuvieri (LeSueur)—Tiger Shark (Leopard Shark). 25 miles south Galveston, Port Arthur and Port Aransas (Baughman and Springer, 1950).

Scoliodon Müller and Henle

S. terraenovae (Richardson)—Sharp-nosed Shark*. Common in the inshore Gulf.

Aprinodon Gill

A. isodon (Müller and Henle)—Smooth-tooth Shark. Texas, (Bigelow and Schroeder, 1948); Laguna Madre and Galveston, (Baughman and Springer, 1950); near Sabine Pass, (Hildebrand, 1954); Laguna Madre, (Simmons, 1957).

Negaprion Whitley

N. brevirostris (Poey)—Lemon Shark*. Aransas Bay, (Gunter, 1945); Texas, (Bigelow and Schroeder, 1948).

Pterolamiops Springer

P. longimanus (Poey)—White-tipped Shark. Apparently common offshore, (Backus, Springer and Arnold, 1956; Springer and Bullis, 1956).

Eulamia Gill

E. floridana (Bigelow, Schroeder and Springer)—Silky Shark. Apparently common offshore, (Springer and Bullis, 1956).

E. milberti (Müller and Henle)—Sand-bar Shark. Texas, (Hildebrand, 1954); Gulf, 600 fathoms, *Oregon* station 1099, (Springer and Bullis, 1956).

E. obscura (LeSueur)—Dusky Shark*. (Shovelnose). Off Padre Island, (Hildebrand, 1954); off Port Aransas, (Baughman, 1950a).

Carcharhinus Blainville

C. acronotus (Poey)—Blacknose Shark*. Near Corpus Christi, (Baughman, 1950a); off Port Aransas, (ML), jaw.

C. leucas (Müller and Henle)—Bull Shark* (Cub Shark). Common in brackish waters and offshore at times, (Baughman, 1950a).

C. limbatus (Müller and Henle)—Blacktip Shark*. Common on Texas beaches, occasionally entering bays. Baughman (1942) has reported *C. natator* Meek and Hildebrand which is probably a subspecies of *limbatus* according to Springer (1950).

C. maculipinnis (Poey)—Large Blacktip Shark. Baughman and Springer (1950) list this species in their key but give no positive evidence for its occurrence in Texas. There is a jaw in the collections of the IMS from off Padre Island and one (ML) from off Port Aransas.

C. porosus Ranzani. Galveston, (Baughman, 1943d as *C. cerdale*); Laguna Madre, (Baughman and Springer, 1950); off St. Joseph's Island and Brazos Santiago, (Hildebrand, 1954). The writer has seen one specimen from off Port Aransas.

SPHYRNIDAE—Hammerhead Sharks

Sphyrna Rafinesque

S. diplana Springer—Hammerhead Shark. Apparently common inshore. Records of *S. zygaena* (Linnaeus) probably refer to this species.

S. tiburo (Linnaeus)—Bonnetnose Shark*. Hildebrand (1954) quotes Gunter in saying this is probably the most common shark in our bays.

S. tudes (Valenciennes)—Great Hammerhead Shark. Off Port Aransas, (Baughman and Springer, 1950), based on a photograph; off St. Joseph's Island, (Hildebrand, 1954).

SQUALIDAE—Dogfishes

Squalus Linnaeus

S. cubensis Howell-Rivero—Cuban Dogfish. Reed (1941) lists *S. acanthias* Linnaeus from Texas: undoubtedly *cubensis* as noted by Baughman and Springer (1950); Gulf, 125 fathoms, *Oregon* station 550, (Springer and Bullis, 1956).

Etmopterus Rafinesque

E. schultzi Bigelow, Schroeder, and Springer. Gulf, 200–400 fathoms, *Oregon* stations 542, 548, 549 (Springer and Bullis 1956).

E. virens Bigelow Schroeder, and Springer. Gulf, 220–260 fathoms, *Oregon* stations 541, 546, (Springer and Bullis, 1956).

SQUATINIDAE—Angel Sharks

Squatina Risso

S. dumerili (LeSueur)—Angel Shark. Apparently uncommon in the shallow Gulf. Baughman (1950a) reports a specimen tentatively identified as *S. argentina* Marini.

PRISTIDAE—Sawfishes

Pristis Link

P. pectinatus Latham—Sawfish* (Common Sawfish). Not uncommon inshore. Baughman (1950a:122) lists records under the second *Pristis pectinatus* Latham.

P. perotteti Müller and Henle—Southern Sawfish. Galveston and Port Isabel, (Baughman, 1943c, 1947) as *Pristis microdon*. Baughman (1950a:122) discusses the species under the first *Pristis pectinatus* Latham, a misprint.

RHINOBATIDAE—Guitarfishes

Rhinobatos Link

R. lentiginosus (Garman)—Atlantic Guitarfish* (Spotted Guitarfish). Not uncommon in shallow water, according to Hildebrand (1954).

TORPEDINIDAE—Electric Rays

Reed (1941) lists *Tetronarce occidentalis* (Storer) from Texas and Baughman (1950a) states that Reed's specimen is in the Chicago Museum of Natural History. A search has failed to reveal the specimen. Probably *Narcine* as Bigelow and Schroeder (1953) do not list this species from the Gulf of Mexico.

Narcine Henle

N. brasiliensis (Olfers)—Lesser Electric Ray. Common in shallow Gulf waters, but not known from bays.

RAJIDAE—Skates

Raja Linnaeus

Bigelow and Schroeder (1954) have described *Raja fuliginea* near Texas waters. It is not known from Texas waters but should be expected here. Reed (1941) lists both *R. eglanteria* and *R. diaphanes* from Texas. There have been no confirmed reports of *R. eglanteria* from Texas and according to Bigelow and Schroeder (1953) *R. diaphanes* does not occur in the Gulf.

R. lentiginosa Bigelow and Schroeder. Gulf, 150 fathoms, *Oregon* station 1094, (Springer and Bullis, 1956).

R. olseni Bigelow and Schroeder. Gulf, 100 fathoms, 27° 20′ N, 96° 20′ W (ML). Gulf, 76 and 65 fathoms, *Oregon* stations 157, 158, (Springer and Bullis 1956).

R. texana Chandler—Texas Skate. Abundant in waters of 10 to 30 fathoms.

Breviraja Bigelow and Schroeder

B. sinusmexicana Bigelow and Schroeder—Short-nosed Skate. Gulf, 200–210 fathoms, *Oregon* stations 162, 1091, 1093, (Springer and Bullis 1956).

ANACANTHOBATIDAE

Springeria Bigelow and Schroeder

S. folirostris Bigelow and Schroeder. Gulf 200 to 260 fathoms, Oregon stations 541, 546, 1091, (Springer and Bullis, 1956).

DASYATIDAE—Sting Rays

Dasyatis Rafinesque

D. americana Hildebrand and Schroeder—Southern Sting Ray. Common in the shallow Gulf, entering bays.

D. sabina (LeSueur)—Sting Ray (Stingaree). Common in bay and inshore waters.

D. sayi (LeSueur)—Sting Ray. Texas, (Hildebrand, 1954). Port Aransas, (IMS). one specimen; Aransas Bay (ML), six specimens.

GYMNURIDAE—Butterfly Rays

Gymnura van Hasselt

G. micrura (Bloch and Schneider)—Butterfly Ray* (Lesser Butterfly Ray). Rare in bays but uncommon in the shallow Gulf.

UROLOPHIDAE

Bigelow and Schroeder (1953) believe that *Urolophus jamaicensis* (Cuvier) should range in the northwestern Gulf. Reed (1941) reports one specimen as *Urobatis sloani* (Blainville) from Texas, but there are no definite records or specimens from Texas. This record was doubted by Baughman (1950a).

MYLIOBATIDAE—Eagle Rays

Evermann and Kendall (1894) and Reed (1941) report *Myliobatis freminvilli* LeSueur. There are no specimens or other records from Texas.

Aetobatus Blainville

A. narinari (Euphrasen)—Spotted Eagle Ray*. Apparently common in the Gulf, Baughman (1950a).

RHINOPTERIDAE—Cow-nose Rays

Rhinoptera Cuvier

R. bonasus (Mitchell)—Cownose Ray*. Common; many have been collected by the staff of the Marine Laboratory in Aransas Bay.

MOBULIDAE—Devil Rays

Manta Bancroft

M. birostris (Donndorff)—Devil Ray* (Giant Devil Ray). Common in the open Gulf; reports based on sight records. Specimens have been brought into Port Aransas.

CHIMAERIDAE—Chimaeras

Hydrolagus Gill

H. alberti Bigelow and Schroeder—Gulf Ratfish. Gulf, 250–400 fathoms, *Oregon* stations 542, 543, (Springer and Bullis, 1956).

LEPISOSTEIDAE—Gars

Lepisosteus Lacépède

Gunter and Knapp (1951) report *L. platostomus* Rafinesque and *L. osseus* (Linnaeus) in waters around two parts per thousand. Hubbs (1957) doubted this record of *platostomus*.

L. productus (Cope)—Spotted Gar*. Uncommon in low salinities, rare in high salinities; Reid (1955) took one specimen from 17 parts per thousand in East Bay.

L. spatula Lacépède—Alligator Gar*. Fairly common in low salinities, the most abundant gar in Texas bays; Gunter (1945) has taken specimens in Gulf waters to 31.2 parts per thousand.

ELOPIDAE—Tarpons

Elops Linnaeus

E. saurus Linnaeus—Bigeye Herring* (Skipjack, ladyfish). Common, the leptocephalus stage entering the bays in the spring.

Megalops Lacépède

M. atlanticus Valenciennes—Tarpon*. Common, entering the bays in summer.

ALBULIDAE—Bonefishes

Albula Bloch and Schneider

A. vulpes (Linnaeus)—Bonefish*. Off Central Texas Coast and 45 miles S. Port Aransas, 116 feet, (Baughman, 1950a, 1955); ESE Port Aransas, 21 fathoms, (Leary, 1957); rare.

CLUPEIDAE—Herrings

Etrumeus Bleeker

E. sadina (Mitchill)—Atlantic Round Herring. Gulf, 85 fathoms, *Oregon* station 1097, (Springer and Bullis, 1956).

E. teres (DeKay)—Round Herring. Gulf, 23, 29 fathoms, *Oregon* stations 1083, 1087, (Springer and Bullis, 1956).

Alosa Cuvier

A. chrysochloris (Rafinesque)—Skipjack Herring* (Blue Herring). See Baughman (1950a); possibly anadromous.

Sardinella Valenciennes

S. anchovia Valenciennes—Spanish Sardine. Galveston, (Fowler, 1945).

Harengula Valenciennes

Baughman (1950a) states that Texas specimens of *H. clupeola* Valenciennes and *H. humeralis* Valenciennes are in the U.S. National Museum. Reports of these species probably refer to the following species as Rivas (1950) did not record either from the northern Gulf.

H. pensacolae Goode and Bean—Pilchard. Common in high salinity waters; Aransas and Copano Bays, Gulf, (Gunter, 1945) as *Harengula macropthalma* (Ranzani); East Bay, (Reid, 1955, 1956, 1957b) as *H. p. pensacolae* Goode and Bean.

Opisthonema Gill

O. oglinum (LeSueur)—Thread Herring. Not uncommon in high salinity waters.

Brevoortia Gill

B. gunteri Hildebrand—Bay Menhaden. Common in bays. (Gunter, 1945) as *Brevoortia* sp.

B. patronus Goode—Gulf Menhaden. This is the common commercial menhaden of our coast. (Gunter, 1945) as *Brevoortia tyrannus* (Latrobe)

Dorosoma Rafinesque

D. petenense (Günther)—Threadfin Shad. A fresh water fish, entering bays.

D. cepedianum (LeSueur)—Gizzard Shad* (Hickory Shad).—Like the former, entering bays.

ENGRAULIDAE—Anchovies

Anchoa Jordan and Evermann

A. hepsetus (Linnaeus)—Anchovy* (Striped Anchovy). Common, leaving the bays during the winter.

A. lyolepis (Evermann and Marsh)—Anchovy*. Lydia Ann Channel and Mustang Island, (Gunter, 1945).

A. mitchilli (Valenciennes)—Anchovy* (Bay Anchovy). Gunter (1945) believed this to be the most abundant fish in numbers on our coast and possibly the most abundant in species mass. The form in our region is *A. m. diaphana* Hildebrand.

ALEPOCEPHALIDAE—Slick-heads

Leptoderma Vaillant

L. macrops Vaillant. Gulf, 300–400 fathoms, *Oregon* stations 543, 549, (Springer and Bullis, 1956).

ARGENTINIDAE—Smelts

Argentina Linnaeus

A. striata Goode and Bean—Argentine. Gulf, 103–210 fathoms, *Oregon* stations 156, 164, 550, 1091, (Springer and Bullis, 1956).

Glossanodon Guichenot

G. pygmaeus Cohen. SE of Port Aransas, (Cohen, 1958).

STERNOPTYCHIDAE—Deep-Sea Hatchetfishes

Gonostoma Rafinesque

G. elongata (Günther). Gulf, 350–400 fathoms, *Oregon* station 543, (Springer and Bullis, 1956).

Yarrella Goode and Bean

Y. blackfordi Goode and Bean. Gulf, 250–400 fathoms, *Oregon* stations 542, 543, 549, (Springer and Bullis, 1956).

Polyipnus Günther

P. asteroides Schultz. Gulf 210–400 fathoms, *Oregon stations* 542, 543, 1093, (Springer and Bullis, 1956).

Sternoptyx Hermann

S. diaphana Hermann. Gulf, 350–400 fathoms, *Oregon* station 543, (Springer and Bullis, 1956).

CHAULIODONTIDAE—Viper-fishes

Chauliodus Bloch and Schneider

C. sloani Bloch and Schneider—Viperfish. Gulf, 250–400 fathoms, *Oregon* stations 542, 549, (Springer and Bullis, 1956).

ASTRONESTHIDAE

Astronesthes Richardson

A. gemmifer (Goode and Bean). Gulf, 300–400 fathoms, *Oregon* station 549, (Springer and Bullis, 1956).

MELANOSTOMIATIDAE—Scaleless Dragonfishes

Echiostoma Lowe

E. margarita Goode and Bean. Gulf, 125 fathoms, *Oregon* station 550, (Springer and Bullis, 1956).

MALACOSTEIDAE—Loosejaws

Photostomias Collett

P. guernei Collett. Gulf, 350–400 fathoms, *Oregon* station 543, (Springer and Bullis, 1956).

SYNODONTIDAE—Lizardfishes

Snyodus Gronow

S. foetens (Linnaeus)—Atlantic lizardfish*. Common in inshore and bay waters.

S. intermedius (Agassiz)—Lizardfish (Sand-diver). Gulf, 18, 23 fathoms, *Oregon* stations 1082, 1083, 1086, (Springer and Bullis 1956).

S. poeyi Jordan—Lizardfish. Off Mustang, St. Joseph's and Padre Islands, (Hildebrand, 1954).

Saurida Valenciennes

S. brasiliensis Norman. Off Padre Island and Corpus Christi Pass, (Hildebrand, 1954). Gulf, 15–29 fathoms, *Oregon* stations 1081, 1082, 1083, 1087, (Springer and Bullis, 1956).

Trachinocephalus Gill

T. Myops (Forster)—Snakefish. Gulf, 18 fathoms, *Oregon* station 1086, (Springer and Bullis, 1956).

SUDIDAE

Chlorophthalmus Bonaparte

Collections by the *Oregon* have taken *C. agassizi* Bonaparte from near Texas waters.

C. chalybeius (Goode). Gulf, 200–210 fathoms, *Oregon* station 1091, (Springer and Bullis, 1956).

C. truculentus Goode and Bean. Gulf, 40–300 fathoms, *Oregon* stations 163, 542, 1088, 1091, (Springer and Bullis 1956).

ALEPISAURIDAE—Lanceletfishes

Alepisaurus Lowe

A. ferox Lowe—Lanceletfish. Gulf, 1000 fathoms, *Oregon* station 1079, (Springer and Bullis, 1956).

MYCTOPHIDAE—Lanternfishes

Diaphus Eigenmann

D. dumerili (Bleeker). Gulf, 220 fathoms, *Oregon* station 541, (Springer and Bullis, 1956).

D. intermedius (Borodin). Gulf, 220 fathoms, *Oregon* station 541, (Springer and Bullis, 1956).

Lampanyctus Bonaparte

L. supralateralis Parr. Gulf, 350–400 fathoms, *Oregon* station 543, (Springer and Bullis, 1956).

Myctophum Rafinesque

M. affine (Lütken). Gulf, 600 and 1050 fathoms, *Oregon* stations 600, 1050, (Springer and Bullis, 1956).

BARBOURIISIDAE

Barbourisa Parr

B. rufa Parr. Gulf, 750 meters, *Atlantis* station 2852, (Parr, 1945).

ARIIDAE—Sea Catfishes

Bagre Oken

B. marina (Mitchill)—Gafftopsail Catfish* (Gafftop). A common fish, marketed commercially, particularly in East Texas.

Galeichthys Valenciennes

G. felis (Linnaeus)—Sea Catfish* (Hardhead). Very abundant, but not normally utilized for food.

ANGUILLIDAE—Fresh-water Eels

Anguilla Shaw

A. rostrata (LeSueur)—American Eel*. Catadromous; not uncommon.

CONGRIDAE—Conger Eels

Congrina Jordan and Hubbs

C. dubius Breder. Gulf, 240–260 fathoms, *Oregon* station 546, (Springer and Bullis, 1956).

C. flava (Goode and Bean). Near Padre Island, (Ginsburg, 1951a); off St. Joseph's Island, (Hildebrand, 1954); Gulf, 45 fathoms, *Oregon* station 5, (Springer and Bullis, 1956).

C. gracilior Ginsburg. Gulf, 45 fathoms, *Oregon* station 5, (Springer and Bullis, 1956).

Neoconger Girard

N. mucronatus Girard. Off Padre Island, Corpus Christi Pass, and St. Joseph's Island, (Ginsburg, 1951a); Off St. Joseph's Island, (Hildebrand, 1954). Girard's type was from off St. Joseph's Island. Apparently not uncommon near shore.

Hoplunnis Kaup

H. macrurus Ginsburg. Hildebrand (1954) found this to be the most abundant eel on the brown shrimp grounds.

H. tenuis Ginsburg. Springer and Bullis (1956); near Port Aransas, (Springer and Hoese, 1958).

Promyllantor Alcock

P. schmitti Hildebrand. Gulf, 350–400 fathoms, *Oregon* station 543, (Springer and Bullis, 1956).

Uroconger Kaup

U. syringinus Ginsburg. Springer and Bullis (1956) report this species near our range; Hildebrand (1954) reports a member of this genus from near Brazos Santiago, off Padre Island, and off Obregon, Mexico, presumably this species.

DYSOMMINIDAE

Dysomma Alcock

D. aphododera Ginsburg. Off Padre Island and off Port Aransas, (Ginsburg, 1951a).

MURAENIDAE—Moray Eels

Baughman (1950a) reports *Gymnothorax funebris* Ranzani on the basis of a sight record—doubtful.

Gymnothorax Bloch

G. moringa (Cuvier)—Speckled Moray*. Galveston and Freeport, (Baughman, 1950a).

G. nigromarginatus (Girard)—Moray. Off Padre Island and St. Joseph's Island, Galveston, (Ginsburg, 1951a); Hildebrand (1954) found this eel abundant in waters from 12 to 34 fathoms.

G. ocellatus Agassiz. Gulf, 39 fathoms, *Oregon* station 551, (Springer and Bullis, 1956).

ECHELIDAE—Worm Eels

Myrophis Lütken

M. punctatus Lütken—Worm Eel. Common on mud bottoms, Ginsburg (1951a) believes the larger eels move offshore.

OPHICHTHIDAE—Snake Eels

Mystriophis Kaup

M. intertinctus (Richardson). Freeport, (Baughman, 1950a); off Corpus Christi Pass, (Hildebrand, 1954).

M. mordax (Poey). Off Padre Island, (Ginsburg, 1951a); Rollover Pass, (Reid, 1957b), Gilchrist (ML).

M. punctifer (Kaup). Freeport and Corpus Christi Pass, (Ginsburg, 1951a).

Ophichthus Ahl

O. gomesi (Castelnau)—Gome's Snake Eel. Not uncommon inshore. Freeport, Port Aransas and Padre Island, (Ginsburg, 1951a); off Sabine Pass, (Hildebrand, 1954); Aransas Bay (ML).

Bascanichthys Jordan and Davis

B. scuticaris (Goode and Bean). Aransas Bay, (Ginsburg, 1951a); Freeport, (Baughman, 1950a).

B. teres (Goode and Bean). Corpus Christi, (Ginsburg, 1951a).

Letarchus Goode and Bean

L. velifer Goode and Bean. Gulf, 240–260 fathoms, *Oregon* station 546, (Springer and Bullis, 1956).

BELONIDAE—Needlefishes

Strongylura van Hasselt

Gunter and Knapp (1951) report specimens of *S. notata* (Poey) and *S. timucu* (Walbaum) taken by Kramer on Mustang Island. There is one specimen in the collections of the IMS identified by Kramer as *timucu*. The specimen is damaged but seems referable to *marina* to this writer. These two species are of doubtful occurrence here as they do not range as far northward on the Atlantic coast as do *marina* and *raphidoma* (Longley and Hildebrand, 1941).

S. longleyi Breder. Gulf, 33 fathoms, *Oregon* station 3, (Springer and Bullis, 1956).

S. marina (Walbaum)—Atlantic Needlefish* (Billfish). Very common, often seen swimming at the surface, particularly at night.

S. raphidoma (Ranzani)—Houndfish. Port Aransas, (IMS).

Ablennes Jordan and Fordice

A. hians (Valenciennes)—Flat Needlefish. Near Port Aransas, (Baughman, 1955); Heald Bank, (Springer and Hoese, 1958).

HEMIRAMPHIDAE—Halfbeaks

Hyporhamphus Gill

H. unifasciatus (Ranzani)—Halfbeak*. Common, appearing in surface waters at night.

Hemiramphus Cuvier

H. brasiliensis (Linnaeus)—Balao. Corpus Christi, (Fowler, 1945).

Euleptorhamphus Gill

E. velox Poey—Flying Halfbeak. Gulf. *Oregon* station 1089, (Springer and Bullis, 1956).

EXOCOETIDAE—Flyingfishes

Cypselurus Swainson

C. cyanopterus (Valenciennes)—Bearded Flyingfish. Corpus Christi, (Fowler, 1945); Gulf, *Oregon* station 1100, (Springer and Bullis, 1956).

C. furcatus (Mitchill)—Fourwing Flyingfish.* (Spot-fin Flyingfish). Gulf, (Breder, 1938); Corpus Christi, (Fowler, 1945); Gulf, *Oregon* stations 1078, 1100, (Spring and Bullis, 1956).

C. heterurus (Rafinesque)—Four-wing Flyingfish (Atlantic Flyingfish). Gulf, *Oregon* stations 1076, 1078, 1100, (Springer and Bullis, 1956).

Prognichthys Breder

P. gibbifrons (Valenciennes)—Bluntnosed Flyingfish. Gulf, (Breder, 1938); Gulf, *Oregon* station 1089, (Springer and Bullis, 1956).

P. rondeleti (Valenciennes)—Blackwinged Flyingfish. Galveston, Port Aransas and Aransas Bay, (Baughman, 1950a); Gulf, *Oregon* stations 1076, 1078, (Springer and Bullis, 1956).

Exocoetus Linnaeus

E. obtusirostris Günther—Twowinged Flyingfish*. Gulf, *Oregon* stations 1076, 1078, 1083, 1100, (Springer and Bullis, 1956).

Oxyporhamphus Gill

O. micropterus (Valenciennes). Gulf, *Oregon* stations 1076, 1100, (Springer and Bullis, 1956) as *O. m. similis* Brunn.

Parexocoetus Bleeker

P. brachypterus (Richardson)—Twowinged Flyingfish* Gulf, *Oregon* stations 1088, 1100, (Springer and Bullis, 1956, as *P. b. hillianus* (Gosse).

BREGMACEROTIDAE

Bregmaceros Thompson

B. atlanticus Goode and Bean. Off Corpus Christi Pass and off Padre Island, (Hildebrand, 1954).

GADIDAE—Codfishes and Hakes

Urophycis Gill

U. floridanus (Bean and Dresel)—Southern Hake. Gunter (1945) discusses this species on our coast.

U. regius (Walbaum)—Spotted Hake*. Gulf, 18 fathoms, *Oregon* station 1086, (Springer and Bullis, 1956).

Phycis Röse

P. cirratus Goode and Bean. Gulf, 100 fathoms, 27° 20′ N, 96° 18′ W, (ML), four specimens.

Gadella Lowe

G. maraldi (Risso). Gulf, 200–400 fathoms, *Oregon* stations 541, 542, 546, 1091, (Springer and Bullis, 1956).

Physiculus Kaup

P. fulvus Bean. Gulf, 100 fathoms, 27° 20′ N, 96° 18′ W, (CNHM No. 45083), one specimen.

MERLUCCIIDAE—Whitings

Merluccius Rafinesque

M. magnoculus Ginsburg—Silver Hake. Off Padre Island, (Ginsburg, 1954); Gulf, 150 fathoms, *Oregon* station 1094, (Springer and Bullis, 1956).

MACROURIDAE—Grenadiers

Bathygadus Günther

B. macrops Goode and Bean. Gulf, 250–400 fathoms, Oregon stations 542, 543, (Springer and Bullis, 1956).

B. vaillanti Roule and Angel. Gulf, 250–400 fathoms, *Oregon* stations 542, 543, (Springer and Bullis, 1956).

Cariburus Parr

C. zaniophorus (Vaillant). Gulf, 350–400 fathoms, *Oregon* station 543, (Springer and Bullis, 1956); collections by the *Oregon* have also taken *C. mexicanus* Parr near Texas waters.

Coelorhynchus Giorna

C. caribbaeus (Goode and Bean). Gulf, 160–210 fathoms, *Oregon* stations 162, 164, 1093, (Springer and Bullis, 1956).

C. carminatus (Goode)—Gulf, 235–300 fathoms, *Oregon* stations 163, 542, (Springer and Bullis, 1956).

Hymenocephalus Giglioli

H. cavernosus (Goode and Bean). Gulf, 200–400 fathoms, *Oregon* stations 163, 542, 1091, (Springer and Bullis, 1956).

Malacocephalus Günther

M. occidentalis (Goode and Bean). Gulf, 200–400 fathoms, *Oregon* station 162, 163, 541, 542, 543, 1093, (Springer and Bullis, 1956).

Nezumia Jordan

N. hildebrandi Parr. Gulf, 350–400 fathoms, *Oregon* station 543, (Springer and Bullis, 1956).

Steindachneria Goode and Bean

S. argentea Goode and Bean. Gulf, 220 fathoms, *Oregon* station 541, (Springer and Bullis, 1956).

FISTULARIIDAE—Cornetfishes

Fistularia Linnaeus

F. tabacaria Linnaeus—Cornetfish. Port Isabel and off Aransas Pass (Baughman, 1950a); off Padre Island, (Hildebrand, 1954). Port Isabel, (ML) two specimens; off Freeport, (FWS) one specimen.

MACRORHAMPHOSIDAE—Snipefishes

Macrorhamphosus Lacépède

M. scolopax (Linnaeus)—Snipefish. Gulf, 125–150 fathoms, *Oregon* stations 550, 1094, (Springer and Bullis, 1956).

SYNGNATHIDAE—Pipefishes and Seahorses

Baughman (1950a) notes the possible presence of *Micrognathus crinigerus* and *Oostethus lineatus* in Texas.

Syngnathus Linnaeus

S. louisianae Günther—Pipefish* (Louisiana Pipefish). Common in areas of vegetation.

S. floridae (Jordan and Gilbert)—Pipefish* (Florida Pipefish). According to Earl Herald (personal communication) the subspecies here is *S. f. floridae* (Jordan and Gilbert). It is common on *Thallasia* flats and other areas of vegetation. Records of *S. mackayi* (Swain and Meek) probably refer to this species.

S. fuscus Storer—Pipefish*. Corpus Christi Pass (USNM No. 132675), Corpus Christi (CNHM No. 40309). According to Herald these specimens represent a relict population in the Corpus Christi area referable to the subspecies *S. f. affinis* Guenther.

S. pelagicus Linnaeus—Pipefish*. For discussion of this species see Springer and Hoese (1958).

S. scovelli (Evermann and Kendall)—Pipefish*. Abundant in areas of vegetation, entering fresh-water.

Hippocampus Rafinesque

H. hudsonius DeKay—Seahorse.* Not uncommon in areas of cover in the bays and shallow Gulf.

H. zosterae Jordan and Gilbert. Not uncommon in bays; records of *H. regulus* are this species.

CYPRINODONTIDAE—Killifishes and Topminnows

Members of this family are all found in the shore zones of the bays and in tidal and marsh pools. All of the marine forms are known to enter or to be able to tolerate fresh-water. Important studies on this group in Texas are Gunter (1950) and Simpson and Gunter (1956).

Lucania Girard

L. parva (Baird and Girard)—Rainwater fish. Not uncommon, found typically along open shores.

Adinia Girard

A. xenica (Jordan and Gilbert)—Diamond Killifish. Copano, Aransas Bays, Aransas Refuge, (Gunter, 1945, 1950); several localities, (Simpson and Gunter, 1956), all as *A. mutifasciata* Girard.

Fundulus Lacépède

Baughman (1950a) reports *F. chrysotus* Holbrook from brackish water but Simpson did not take it in his extensive study (Simpson and Gunter, 1956). Dr. Gunter (personal communication) has never taken *chrysotus* from salt water and neither has the writer. Kilby (1955) has taken two specimens from brackish water in Florida.

F. grandis Baird and Girard—Gulf Killifish. Common all along the coast; *F. pallidus* Evermann is probably a synonym.

F. jenkinsi (Evermann)—Blackspot Topminnow.* According to Simpson and Gunter (1956) this is a rare form in low salinities from the eastern coast of Texas.

F. pulvereus (Evermann)—Bayou Killifish. Baughman (1950a) believed this fish to be common, but Gunter (1950) and Simpson and Gunter (1956) found it to be rare. Clark Hubbs (personal communication) believes it is locally abundant. Miller (1955) gives the range from Alabama to Corpus Christi.

F. similis (Baird and Girard)—Longnose Killifish. Common in medium to high salinities.

Cyprinodon Lacépède

C. variegatus Lacépède—Variegated Cyprinodon* (Sheepshead Minnow). Gunter (1945) showed that this species was second in numbers only to *Menidia beryllina* in shore zones, and subsequently (1950) that it was the most abundant fish in salt ponds. It has been taken from fresh-waters to waters of 140 parts per thousand (Gunter, 1956).

POECILIIDAE—Mosquitofishes

Gambusia Poey

G. affinis (Baird and Girard)—Gambusia* (Common Mosquitofish). A fresh-water fish able to tolerate high salinities.

Mollienesia LeSueur

M. latipinna LeSueur—Sailfin Molly.* A fresh-water fish, native to the coastal region, able to tolerate high salinities. *M. formosa*, probably originating as a hybrid between *latipinna* and *M. sphenops*, has never been reported from salt waters, but should be expected there in South Texas.

POLYMIXIDAE—Barbudos

Polymixia Lowe

P. lowei Günther. Gulf, 160–210 fathoms, *Oregon* stations 164, 1091, 1093, 1094, (Springer and Bullis, 1956).

TRACHICHTHYIDAE

Hoplostethus Cuvier

H. mediterraneus Cuvier. Gulf, 210 fathoms, *Oregon station* 1093, (Springer and Bullis, 1956).

HOLOCENTRIDAE—Squirrelfishes

Holocentrus Scopoli

H. ascensionis (Osbeck)—Squirrelfish*. Port Isabel, (Baughman, 1947); Port Aransas, (Gunter and Knapp, 1951).

ZEIDAE—Dories

Zenion Jordan and Evermann

Z. hololepis (Goode and Bean). Gulf, 200–300 fathoms, *Oregon* stations 542, 1091, 1093, (Springer and Bullis, 1956).

Zenopsis Gill

Z. ocellata (Storer). 27° 20′ N, 96° 18 W, 100 fathoms, (ML), one specimen.

Cyttopsis Gill

C. roseus (Lowe). Gulf, 210–260 fathoms, *Oregon* stations 541, 546, 1093, (Springer and Bullis, 1956).

ANTIGONIIDAE

Antigonia Lowe

A. capros Lowe. Gulf, 103 fathoms, *Oregon* station 156, (Springer and Bullis, 1956).

SPHYRAENIDAE—Barracudas

Sphyraena Rose

Baughman (1950b) has reported *S. picudilla* Poey based on a tentative identification. There are no positive records of its occurrence in Texas waters to the writer's knowledge.

S. barracula (Walbaum)—Great Barracuda*. Port Isabel, (Baughman, 1947).

S. guachancho Cuvier—Guaganche (Little Barracuda). Aransas Bay, (Gunter, 1945); No locality, (Baughman, 1950b); off Padre Island and Pass Cavallo, (Hildebrand, 1954); Aransas Bay, (ML).

MUGILIDAE—Mullets

Mugil Linnaeus

M. cephalus Linnaeus—Striped Mullet*. Abundant, running up streams.

M. curema Valenciennes—White Mullet*. Fairly abundant; but not as common as *cephalus*.

ATHERINIDAE—Silversides

Menidia Bonaparte

M. beryllina (Cope)—Atlantic Silversides*. Gunter (1945) found this to be the dominant inshore species in Texas bays.

Membras Bonaparte

M. martinica (Valenciennes)—Rough Silversides. Abundant along bay shores in high salinities.

POLYNEMIDAE—Threadfins

Polydactylus Lacépède

P. octonemus (Girard)—Threadfin* (Eightfingered threadfin). Abundant inshore, occasionally entering bays.

CENTROPOMIDAE—Snooks

Centropomus Lacépède

C. undecimalis (Bloch)—Snook*. Not uncommon, entering fresh-water.

SERRANIDAE—Sea Basses and Groupers

Chorististium Gill

C. sp. There are two specimens of this genus (*Liopropoma aberrans* (Poey) of authors) from Texas, (CNHM Nos. 45164–65) collected by McRae.

Epinephelus Bloch

E. adscensionis (Osbeck)—Rock Hind*. Snapper Banks, (Baughman, 1943a); Port Aransas Jetties, (IMS), Snapper banks, (ML).

E. drummondhayi Goode and Bean—Speckled Hind. Texas, (Reed, 1941); Port Isabel, (Baughman, 1947).

E. morio (Cuvier)—Red Grouper. Texas, (Reed, 1941); Gulf, 35 fathoms, *Oregon* station 556, (Springer and Bullis, 1956).

E. striatus (Bloch)—Nassau Grouper*. Texas, (Reed, 1941); Mustang Island, (Gunter and Knapp, 1951).

Garrupa Jordan

G. nigrita (Holbrook)—Black Grouper*. Fairly common, young entering bays.

Promicrops Gill

P. itaiara (Lichtenstein)—Spotted Jewfish*. Not uncommon; Hildebrand (1954) discusses this species on our coast.

Mycteroperca Gill

M. bonaci (Poey)—Black Grouper*. According to Henry Hildebrand (personal communication) this is very common around the Port Aransas jetties.

M. falcata (Poey)—Scamp. Freeport and Aransas Pass, (Baughman, 1943a); Gulf, 55 fathoms, *Oregon* station 6, (Springer and Bullis, 1956).

M. microlepis (Goode and Bean)—Gag. Texas, (Reed, 1941); Freeport and Galveston, (Baughman, 1943a); Port Aransas, (Gunter and Knapp, 1951).

M. interstitialis (Poey)—Princess Rockfish. Port Aransas jetties, (IMS) one specimen.

Anthiasicus Ginsburg

A. leptus Ginsburg. Gulf, 150 fathoms, *Oregon* station 1094, (Springer and Bullis, 1956).

Centropristes Cuvier

Weed (1937) reports *C. springeri* Weed from Texas and Ginsburg (1952a) subsequently synonymized *springeri* with *ocyurus*. One of the paratypes of *springeri* came from off Galveston.

C. philadelphicus (Linnaeus)—Rock Sea Bass. Not uncommon in the shallow Gulf according to Hildebrand (1954). Reed's (1941) *striatus* was probably this species.

Serraniculus Ginsburg

S. pumilio Ginsburg. Texas, (Ginsburg, 1952a); off Padre Island, (Hildebrand, 1954).

Diplectrum Holbrook

D. arcuarium Ginsburg. Port Isabel, (Ginsburg, 1948); Texas, (Hildebrand, 1954); 13½ fathoms southeast Galveston, (ML). This form was described by Ginsburg (1948) as a subspecies of either *radiale* or *bivittatum* pending further study.

D. formosum (Linnaeus)—Sandfish. Snapper Banks, (Gunter, 1941); Freeport and Galveston, (Baughman, 1944, 1950b).

Hemianthias Steindachner

H. vivanus (Jordan and Swain)—Red Barbier. Gulf, 18, 125 fathoms, *Oregon* stations 550, 1086, (Springer and Bullis, 1956).

Prionodes Jenyns

Prionodes phoebe (Poey) has been collected by T. R. Leary off Calcasieu, Louisiana, and it should be expected here.

P. pomospilus (Ginsburg). Off Padre Island and St. Joseph's Island and off Corpus Christi Pass, (Ginsburg, 1952a); Texas, (Hildebrand, 1954), both as *Paracentropristes pomospilus*.

Parepinephelus Bleeker

P. acutirostris (Cuvier). Corpus Christi, (Woods, 1942).

Rypticus Cuvier

R. saponaceus (Bloch and Schneider)—Three-spined soapfish. 50 fathoms off Freeport, (Baughman, 1943a).

Hypoplectrus Gill

H. chlorurus (Cuvier)—Butter Hamlet. Corpus Christi, (Woods, 1942); Port Aransas, (Gunter and Knapp, 1951), as *H. unicolor* (Walbaum).

Serranellus Jordan

S. subligarius (Cope)—Belted Sandfish. Corpus Christi, (Woods, 1942); Port Aransas, (Baughman, 1947), both as *Dules subligaris.*

PRIACANTHIDAE—Big-eyes

Priacanthus Cuvier

P. arenatus Cuvier—Common Big-eye. Off Port Aransas, (Baughman, 1950b); Texas, 20–25 fathoms, (Gunter and Knapp, 1951); off Padre Island, (Hildebrand, 1954),

APOGONIDAE—Cardinalfishes

Synagrops Günther

S. bella (Goode and Bean). Gulf, 150–300 fathoms, *Oregon* stations 542, 1094, (Springer and Bullis, 1956).

S. spinosa Schultz. 27° 15′ N, 96° 15′ W, 200 fathoms (CNHM No. 45131), one specimen.

Epigonus Rafinesque

E. pandionis (Goode and Bean). Gulf, 210 fathoms, *Oregon* station 1093, (Springer and Bullis, 1956).

Apogon Lacépède

A. aurolineatus (Mobray). 27° 30′ N, 96° 28′ W, 40 fathoms, (CNHM No. 54130), one small specimen tentatively identified as this species.

BRANCHIOSTEGIDAE—Tilefishes

Lopholatilus Goode and Bean

L. chamaeleontion Goode and Bean. Tilefish.* Gulf, 125–150 fathoms, *Oregon* stations 550, 1094, (Springer and Bullis, 1956).

Caulolatilus Gill

C. cyanops Poey—Ocean Whitefish. Off Padre Island, (Hildebrand, 1954); Gulf, 58 fathoms, *Oregon* station 159, (Springer and Bullis, 1956).

C. intermedius Howell-Rivero—Whitefish. 91 fathoms SE of Port Aransas (ML), two specimens.

MALACANTHIDAE—Blanquillos

Malacanthus Cuvier

M. plumieri (Bloch)—Sandfish. Off Port Isabel, off Port Aransas, (Baughman, 1947, 1950b).

POMATOMIDAE—Bluefishes

Pomatomus Lacépède

P. saltatrix (Linnaeus)—Bluefish*. Not uncommon, at one time supporting a fishery in the eastern portion of the state.

RACHYCENTRIDAE—Sergeantfishes

Rachycentron Kaup

R. canadus (Linnaeus)—Cabio* (Ling, Cobia). Common in the open Gulf, the young entering bays.

CARANGIDAE—Jacks, Scads, and Pompanos

Seriola Cuvier

S. dumerili (Risso)—Amberjack* (Great Amberjack). Near Port Aransas, (Gunter and Knapp, 1951). Baughman's (1941) records of *S. lalandi* were probably this species.

Elagatis Bennett

E. bipinnulatus (Quoy and Gaimard)—Rainbow Runner. Near Port Aransas, (Gunter and Knapp, 1951).

Trachinotus Lacépède

T. carolinus (Linnaeus)—Common Pompano*. Common, see Baughman (1950b).

T. falcatus (Linnaeus)—Round Pompano*. Rockport, (Baughman, 1941); off Mustang Island, (Gunter and Knapp, 1951); Corpus Christi and Aransas Pass, (Ginsburg, 1952b). Gunter and Knapp's (1951) *T. goodei* was probably a large *falcatus*, following Ginsburg (1952b).

T. glaucus (Bloch)—Longfin Pompano*. Corpus Christi, (Fowler, 1931); Mustang Island, (Gunter, 1945); Mustang Island, (Gunter and Knapp, 1951); both as *T. palometa* Regan; (Ginsburg, 1952b).

Selar Bleeker

S. crumenophthalmus (Bloch)—Bigeye Scad*. Gulf, 18, 50 fathoms, *Oregon* stations 2, 1086, (Springer and Bullis, 1956); Pass Cavallo, (Hildebrand, 1954).

Trachurus Rafinesque

T. lathami Nichols—Rough Scad. Apparently not uncommon. Galveston and Port Aransas, (Baughman, 1941); Port Aransas, (Gunter, 1945); Baffin Bay, Port Aransas, and Mustang Island, (Ginsburg, 1952b).

Caranx Lacépède

C. bartholomaei Cuvier—Yellow Jack*. St. Joseph's Island, (Gunter and Knapp, 1951).

C. crysos (Mitchill)—Blue Runner*. Port Arthur, Galveston, and Freeport, (Baughman, 1941), as *Paratractus crysos*.

C. hippos (Linnaeus)—Common Jack*. (Cavalla, Jack Crevalle). Common, entering bays.

C. latus Agassiz—Horse-eye Jack. Freeport and Galveston (Baughman, 1941), as *Xurellata;* Mustang Island (Gunter and Knapp, 1951); Padre Island (Ginsburg, 1952b).

C. ruber (Bloch)—Skipjack. Port Isabel, (Baughman, 1947), Gulf, 50 fathoms, *Oregon* station 2 (Springer and Bullis, 1956).

Hemicaranx Bleeker

H. amblyrhynchus (Cuvier)—Blunt-nosed Jack. Common accompanying large numbers of jellyfish.

Chloroscombrus Girard

C. chrysurus (Linnaeus)—Bumber*. Common; (Baughman, 1950b) reports the young from the bell of *Stomolophus*.

Alectis Rafinesque

A. crinitus (Mitchill)—Threadfish*. Off Port Aransas, (Springer and Hoese, 1958).

Vomer Cuvier

V. setapinnis (Mitchill)—Moonfish*. Common, entering bays.

Selene Lacépède

S. vomer (Linnaeus)—Lookdown*. Common, entering bays.

Oligoplites Gill

O. saurus (Bloch and Schneider)—Leatherjacket*. Uncommon in bays and the shallow Gulf.

CORYPHAENIDAE—Dolphins

Coryphaena Linnaeus

C. hippurus Linnaeus—Dolphin*. Common, young entering bays (Pew, 1957).

C. equisetis Linnaeus—Little Dolphin*. Gulf, *Oregon* stations 1078, 1089, 1100, (Springer and Bullis, 1956).

LUTIANIDAE—Snappers

Lutianus Bloch

L. analis (Valenciennes)—Muttonfish*. Texas (Baughman, 1943b); Gulf, 18 fathoms, *Oregon* station 1086 (Springer and Bullis, 1956).

L. apodus (Walbaum)—Schoolmaster*. Near Corpus Christi (Baughman, 1950b); Aransas Pass and Aransas Bay (Gunter and Knapp, 1951).

L. aya Bloch—Red Snapper*. This is the common commercial snapper of our coast. We follow Camber (1955) in the use of the name *aya* over *blackfordi*.

L. griseus (Linnaeus)—Gray Snapper* (Mangrove Snapper). Fairly common, the only snapper regularly entering bays.

L. synagris (Linnaeus)—Lane Snapper*. Snapper banks, (Baughman, 1943b); Corpus Christi, (Fowler, 1945); Texas Gulf, (Hildebrand, 1954); occasional specimens are taken inshore.

Ocyurus Gill

O. chrysurus (Bloch)—Yellowtail Snapper*. Gulf, 103 fathoms, *Oregon* station 156, (Springer and Bullis, 1956).

Rhomboplites Gill

R. aurorubens (Cuvier)—Vermillion Snapper. Probably common on the snapper banks. Baughman (1947, 1950b); Hildebrand (1954), and Springer and Bullis (1956) list records.

Pristipomoides Bleeker

P. andersoni Ginsburg. Very common offshore. Baughman (1950b), as *P. macrophthalmus* (Müller and Troschel); Hildebrand (1954) and Springer and Bullis (1956) have other records.

LOBOTIDAE—Tripletails

Lobotes Cuvier

L. surinamensis (Bloch)—Tripletail*. Fairly common along the coast, frequently lying on the surface.

GERRIDAE—Mojarras

Eucinostomus Baird and Girard

The taxonomy of this genus is little understood. Two species with three anal spines are fairly common, and a third with two anal spines has been taken. Gunter (1945) reported *Gerres rhombeus* which was in error according to Gunter and Knapp (1951).

E. argenteus Baird and Girard—Mojarra*. Copano and Aransas Bays, (Gunter, 1945), as *E. californiensis* (Gill); off Padre and Mustang Islands, (Hildrebrand, 1954).

E. gula (Cuvier)—Mojarra*. Copano and Aransas Bays. (Gunter, 1945); Hildebrand (1954) found this species to be very common.

E. lefroyi (Goode)—Mojarra*. Specimens tentatively identified as this species have been collected by V. G. Springer from Port Aransas and by the writer from Aransas Bay. There is a specimen in the collections of the IMS from Padre Island identified by Henry Hildebrand.

Xystaema Jordan and Evermann

X. cinereum (Walbaum)—Mojarra*. Copano and Aransas Bays, (Baughman, 1950b), (ML); Laguna Madre, (Simmons, 1957), probably some were *Eucinostomus* spp. The specimen of *Gerres brasiliensis* Cuvier reported by Baughman (1950b) in the CNHM is this species.

HAEMULIDAE—Grunts

Reed (1941) reports *Haemulon macrostomum* Günther and *H. parra* (Desmarest) from Texas but these have not been reported since. Probably some species of *Haemulon* do occur on offshore reefs and banks but until this is verified it seems wise not to include these in the Texas fauna.

Conodon Cuvier

C. nobilis (Linnaeus)—Barred Grunt. Fairly common in the shallow Gulf.

Pomadasys Lacépède

P. crocro (Cuvier)—Snapper reef, south of Port Aransas, (Gunter and Knapp, 1951).

Bathystoma Scudder

B. aurolineatum (Cuvier)—Tomtate* (Yellow Tomtate). Heald Bank, (Baughman, 1950b), as *B. rimator* (Jordan and Swain); off Padre Island, (Hildebrand, 1954), as *B. a. rimator* (Jordan and Swain).

Anisotremus Gill

A. surinamensis (Bloch)—Black Margate*. Port Isabel and Port Aransas. (Baughman, 1945).

Orthopristis Girard

O. chrysopterus (Linnaeus)—Pigfish* (Big Perch). Common in bays and shallow Gulf.

SCIAENIDAE—Croakers

Eques Bloch

E. acuminatus (Bloch and Schneider)—Ribbonfish. Gulf, 20, 30 fathoms, *Oregon* stations 536, 537, (Springer and Bullis, 1956).

Larimus Cuvier

L. fasciatus Holbrook—Banded Drum* (Banded Croaker). Uncommon in the shallow Gulf.

Bairdiella Gill

B. chrysura (Lacépède)—Silver Perch*. Not uncommon in bays and the shallow Gulf.

Stellifer Oken

S. lanceolatus (Holbrook)—Star Drum*. Not uncommon in high salinity waters.

Sciaenops Gill

S. ocellata (Linnaeus)—Red Drum* (Redfish). Common on grass flats, utilized commercially.

Leiostomus Lacépède

L. xanthurus Lacépède. Spot*. (Spot Croaker, Flat Croaker). Very common in bays and the shallow Gulf.

Micropogon Cuvier

According to Gordon Gunter (personal communication) *M. furnieri* (Desmarest) possibly occurs in the Port Isabel area, however, there is no positive evidence of its occurrence in Texas.

M. undulatus (Linnaeus)—Atlantic Croaker*. One of our most abundant fishes.

Menticirrhus Gill

M. americanus (Linnaeus)—Southern Kingfish. Common in the shallow Gulf, entering bays.

M. focaliger Ginsburg—Gulf Minkfish. Hildebrand (1954) reports this species for the first time for the western Gulf and Texas.

M. littoralis (Holbrook)—Gulf Kingfish. Not uncommon in the shallow Gulf.

Pogonias Lacépède

P. cromis (Linnaeus)—Black Drum*. Another commercially important sciaenid, more abundant in southern Texas waters.

Cynoscion Gill

Some authors place this genus in a separate family (Otolithidae).

C. arenarius Ginsburg—Sand Squeteague* (Sand Trout). Common in bay and shallow Gulf areas.

C. nebulosus (Cuvier)—Spotted Squeteague* (Speckled Trout). The common commercial and largest member of this genus on our coast.

C. nothus (Holbrook)—Silver Squeteague* (Silver Trout). Common in the shallow Gulf.

SPARIDAE—Porgies

Stenotomus Gill

S. caprinus Bean—Longspined Porgy*. Common in the shallow Gulf, (Gunter and Knapp, 1951; Hildebrand, 1954; Caldwell, 1955).

Calamus Swainson

The members of this genus are little understood. The following species have been reported, and until this genus is revised it seems wise to retain these records.

C. bajonada (Bloch and Schneider)—Jolthead Porgy*. Heald Bank, (Baughman, 1950b).

C. calamus (Valenciennes)—Saucereyed Porgy*. Mustang Island, (Gunter and Knapp, 1951).

C. macrops Poey. Galveston and Freeport, (Baughman, 1950b).

C. penna (Valenciennes)—Sheepshead Porgy. Galveston, (Baughman, 1950b).

C. leucosteus Jordan and Gilbert—White-boned Porgy. Hospital reef, (Gunter and Knapp, 1951), (AM).

Lagodon Holbrook

L. rhomboides (Linnaeus)—Pinfish* (Pin Perch). Abundant in inshore waters.

Archosargus Gill

A. probatocephalus (Walbaum)—Sheepshead*. Ginsburg (1952a) described a new species, *oviceps*, from the western Gulf based on the number of body bands—5 in *oviceps* and 6 in *probatocephalus*. Hildebrand (1955) subsequently found western Gulf sheepshead with six bands and synonymized the two species. The writer has seen specimens from Texas with 6 bands. These differences are noteworthy but not of species magnitude as noted by Hildebrand (1955).

MULLIDAE—Goatfishes

Mullus Linnaeus

M. auratus Jordan and Gilbert. Gulf, 50 fathoms, *Oregon* station 2, (Springer and Bullis, 1956).

Upeneus Cuvier

U. parvus (Poey). Not uncommon in the shallow Gulf according to Gunter and Knapp (1951) and Hildebrand (1954).

KYPHOSIDAE—Chopas

Kyphosus Lacépède

K. sectatrix (Linnaeus)—Bermuda Chub*. Corpus Christi, (Fowler, 1931); Texas, (Baughman, 1950b); Port Aransas Jetties, (Baughman, 1947), (ML), two specimens.

EPHIPPIDAE—Spadefishes

Chaetodipterus Lacépède

C. faber (Broussonet)—Spadefish*. Common in the shallow Gulf, the young entering bays.

ANTIGONIIDAE—Boarfishes

Antigonia Lowe

A. capros Lowe. Gulf, 103 fathoms, *Oregon* station 156, (Springer and Bullis, 1956).

CHAETODONTIDAE—Butterflyfishes

Chaetodon Linnaeus

C. ocellatus Bloch—Butterflyfish* (Common Butterflyfish). Port Isabel, Lydia Ann Channel, (Baughman, 1947, 1950b); Port Aransas jetties, (Hildebrand, 1955).

Holacanthus Lacépède

H. isabelita (Jordan and Rutter)—Common Angelfish. Port Aransas, (Springer and Hoese, 1958).

Pomacanthus Lacépède

P. paru (Bloch)—French Angelfish. Aransas Bay, (Springer and Hoese, 1958).

POMACENTRIDAE—Demioselles

Pomacentrus Lacépède

P. leucostictus Müller and Troschel. Off Pass Cavallo, (Springer and Hoese, 1958).

Abudefduf Forskål

A. saxatilis (Linnaeus)—Sergeant major. Port O'Connor, (Baughman, 1950b) as *A. marginatus* (Bloch); Port Aransas Jetties, (Gunter and Knapp, 1951).

LABRIDAE—Wrasses

Gunter (1944) discusses the error concerning the capitaine, *Lachnolaimus maximus* (Walbaum), and states that it does occur on offshore reefs, but apparently there are no positive records or specimens in collections from Texas.

Halichoeres Rüpell

H. bivittatus (Bloch)—Slippery Dick. Port Aransas, (Springer and Hoese, 1958).

Decodon Günther

D. puellaris (Poey). 27° 20′ N, 96° 20′ W, 100 fathoms, (CNHM No. 45238) five specimens.

SCARIDAE—Parrotfishes

Sparisoma Swainson

S. radians (Valenciennes)—Radiant Parrotfish. Corpus Christi Bay, (Leary, 1956); Port Isabel, (Springer and Hoese, 1958).

OPISTHOGNATHIDAE—Jawfishes

Lonchopisthus Gill

L. linderi Ginsburg—Jawfish. Off Padre Island, (Ginsburg, 1942); Sebree Bank, (Hildebrand, 1954).

PERCOPHIDIDAE

Bembrops Steindachner

B. anatirostris Ginsburg. Gulf, 150–210 fathoms, *Oregon* stations, 1093, 1094, 1095, (Springer and Bullis, 1956).

B. gobioides (Goode). Gulf, 200–230 fathoms, *Oregon* stations, 163, 1091, 1093, (Springer and Bullis, 1956).

URANOSCOPIDAE—Electric Star-gazers

Astroscopus Brevoort

A. y-graecum (Cuvier)—Stargazer* (Southern Stargazer). Common on beaches as noted by Baughman (1950b).

Kathetostoma Günther

K. albigutta (Bean). Not uncommon in deep waters. Off Port Aransas, (Baughman, 1950b); Hildebrand (1954) and Springer and Bullis (1956) supply other records.

Benthoscopus Longley and Hildebrand

B. laticeps Longley and Hildebrand. 27° 20′ N, 96° 18′ W, 100 fathoms, (CNHM No. 45247), one specimen.

BLENNIIDAE—Blennies

The rocky and shell habitats of the Texas coast contain a rich fauna of blennies, much of which has not been adequately studied. Baughman (1950b) has reported *Rupiscartes atlanticus* (Valenciennes). This record seems doubtful.

Blennius Linnaeus

B. cristatus Linnaeus—Molly Miller. Port Aransas jetties, (Baughman, 1947); this species is common on the jetties. The writer has seen one specimen from Galveston.

Hypleurochilus Gill

H. geminatus (Wood)—Crested Blenny. See Baughman (1950b) for Texas records of this form.

Hypsoblennius Gill

Baughman (1950b) lists the records of the two closely related species of this genus reported from Texas.

H. hentzi (LeSueur)—Carolina Blenny

H. ionthas (Jordan and Gilbert). Freckled Blenny.

Chasmodes Valenciennes

Fowler (1945) reported *C. saburrae* Jordan and Gilbert from Flour Bluff. The taxonomy of this genus is not well understood and is presently being revised by Victor Springer. All Texas specimens known to this writer are referable to the following species.

C. bosquianus (Lacépède)—Striped Blenny. Corpus Christi, (Evermann and Kendall, 1894), Fulton, Copano and East Bays (ML).

CLINIDAE—Kelpfishes

Labrisomus Swainson

L. nuchipinnis (Quoy and Gaimard)—Hairy Blenny (Hairy Head). Port Aransas jetties, (Baughman, 1947). This species is abundant on these and the Port Isabel jetties.

MICRODESMIDAE

Microdesmus Günther

M. sp. Baughman (1950b) believes that *M. longipinnis* (Weymouth) occurs in Texas waters as it has been collected off Cameron, Louisiana; Henry Hildebrand took one specimen in Texas waters which did not agree with Weymouth's description. There is one specimen (ML) taken from Cedar Bayou, which agrees with the description

of *longipinnis*, except in having fewer myomeres. More specimens are needed to delimit the species.

OPHIDIIDAE—Cusk Eels

Lepophidium Gill

L. brevibarbe (Cuvier)—Shortbearded Cusk Eel. Gunter and Knapp (1951) and Hildebrand (1954) found this form to be not uncommon offshore.

Ophidion Linnaeus

O. holbrooki (Putnam)—Holbrook's Cusk Eel. Heald Bank, (Nichols and Breder, 1922).

Rissola Jordan and Evermann

R. marginata (DeKay)—Northern Slippery Dick. See Baughman (1950b) for a list of Texas records.

Otophidium Gill

O. welshi Nichols and Breder—Welsh's Cusk Eel. Gunter and Knapp (1951) summarize the status of this species in Texas waters.

BROTULIDAE—Brotulid Fishes

Brotula Cuvier

B. barbata (Bloch and Schneider)—Brotula. Texas, (Baughman, 1950b); Texas, (Hildebrand, 1954); off Port Aransas, Laguna Madre, (ML).

Dicrolene Goode and Bean

D. intronigra Goode and Bean. Gulf, 350–400 fathoms, *Oregon* stations 43, (Springer and Bullis, 1956).

Neobythites Goode and Bean

N. marginatus Goode and Bean. Gulf, 150 fathoms, *Oregon* station 1094, (Springer and Bullis, 1956).

CALLIONYMIDAE—Dragonnets

Callionymus Linnaeus

C. agassizi Goode and Bean. Gulf, 103 fathoms, *Oregon* station 156, (Springer and Bullis, 1956), as *C. himantophorus* Goode and Bean.

TRICHIURIDAE—Cutlassfishes

Trichiurus Linnaeus

T. lepturus Linnaeus—Atlantic Cutlassfish*. Common in the shallow Gulf and bays.

SCOMBRIDAE—Mackerels and their allies

Scomber Linnaeus

S. colias Gmelin—Chub Mackerel. Off Padre and Mustang Islands, (Hildebrand, 1954); off Port Isabel, (Baughman, 1955), as *Pneumatophorus colias* (Gmelin).

Auxis Cuvier

A. thazard (Lacépède)—Frigate Mackerel. Gulf, 40 fathoms, *Oregon* station 1088, (Springer and Bullis, 1956). These are larval and young specimens according to Harvey Bullis (personal communication).

Katsuwonus Kishinouye

K. pelamis (Linnaeus)—Oceanic Bonito*. Sight record from Port Isabel, (Baughman, 1950b); Gulf, *Oregon* station 1099, (Springer and Bullis, 1956).

Euthynnus Lütken

E. alieterattus (Rafinesque)—Little Tuna*. Texas, (Reed, 1941); Gulf 50 fathoms, *Oregon* station 2, (Springer and Bullis, 1956).

Thunnus South

T. atlanticus (Lesson)—Atlantic Blackfin Tuna*. Port Isabel, (Baughman, 1941).

T. thynnus (Linnaeus)—Bluefin Tuna*. Off Port Aransas, (Springer and Hoese, 1958).

T. albacares (Bonnaterre)—Atlantic Yellowfin Tuna*. Although there are no positive records for the occurrence of *albacares* in Texas waters, undoubtedly it occurs here as they have been caught very near our waters (Springer and Bullis, 1956), and Mr. A. R. Brundrett, taxidermist at Port Aransas, claims to have mounted the species. There have been newspaper releases and magazine articles referring to catches of Texas tuna.

Sarda Cuvier

S. sarda (Bloch)—Atlantic Bonito*. See Baughman (1950b) for the list of Texas records.

Scomberomorus Lacépède

S. cavalla (Cuvier)—King Mackerel*. Texas, (Baughman, 1941, 1950b).

S. maculatus (Mitchill)—Spanish Mackerel*. Not uncommon, entering bays.

S. regalis (Bloch)—Cero*. See Baughman (1950b) for a discussion of Texas records.

Acanthocybium Gill

A. solandri Cuvier—Wahoo*. Freeport, Port Isabel, and Port Aransas, (Baughman, 1941, 1950b).

ISTIOPHORIDAE—Sailfishes

Tetrapturus Rafinesque

T. belone Rafinesque—Spearfish. Off Port Aransas, (Springer and Hoese, 1958).

Istiophorus Lacépède

I. americanus (Cuvier)—Atlantic Sailfish*. There are many records of this species off the Texas coast. Springer and Hoese (1958) have recently described a young sailfish from off Port Aransas.

Makaira Lacépède

M. albida (Poey)—White Marlin*. Off Port Aransas, (Baughman, 1941, 1950b), sight records. There have been a number taken off Port Aransas.

M. ampla (Poey)—Blue Marlin*. This species has been taken off the Port Isabel and Port Aransas areas.

XIPHIIDAE—Swordfishes

Xiphias Linnaeus

X. gladius Linnaeus—Broadbill Swordfish*. Padre Island, (Kramer, 1950).

STROMATEIDAE—Harvestfishes

Peprilus Cuvier

P. paru (Linnaeus)—Harvestfish*. Common, entering bays; *P. burti* Fowler 1944, is probably a synonym.

Poronotus Gill

P. triacanthus (Peck)—Butterfish*. Common, entering bays.

Cubiceps Lowe

C. nigriargenteus Ginsburg. 27° 15′ N, 96° 15′ W, 200 fathoms (CNHM No. 45129). There are six specimens tentatively identified as this species.

NOMEIDAE—Man-of-war Fishes

Nomeus Cuvier

N. gronovi (Gmelin)—Man-of-war Fish. Port Aransas and Galveston, (Baughman, 1950b); Galveston, (ML), one specimen; Port Aransas, (IMS), two specimens.

Psenes Cuvier

P. pellucidus Lütken. Gulf, *Oregon* station 1078, (Springer and Bullis, 1956).

ELEOTRIDAE—Sleepers

Dormitator Gill

D. maculatus (Bloch)—Fat Sleeper. Chambers County, (Baughman, 1946). During the heavy rains of 1957 many have been collected in Texas bays from Sabine Lake to Galveston by members of the Game and Fish Commission. The writer has seen specimens collected from tide pools near Rockport.

Eleotris Bloch and Schneider

E. pisonis (Gmelin)—Spinycheek Sleeper. Mission Bay, (Baughman, 1950b), the writer has seen one specimen from Galveston.

Gobiomorus Lacépède

G. dormitor Lacépède—Metapil. Rio Grande, (Evermann and Kendall, 1894); Arroyo Colorado, (ML), one specimen; Al Flury of the Texas Game and Fish Commission has reported two specimens from the Aransas River, (Job Completion Report, Texas Game and Fish Commission Project No. F6R3, Job B–6).

GOBIIDAE—Gobies

Gobionellus Girard

G. boleosoma (Jordan and Gilbert)—Darting Goby. Texas, (Ginsburg, 1932); Galveston and Corpus Christi, (Gunter, 1941); Copano and Aransas Bays, (Gunter, 1945).

G. gracillimus Ginsburg. Off Padre Island and Green's Bayou, (Hildebrand, 1954).

G. hastatus Girard—Sharptail Goby. Not uncommon. Records of *G. oceanicus* (Pallas) probably refer to this species.

G. shufeldti (Jordan and Eigenmann)—Freshwater Goby. Dickinson Bayou, (Ginsburg, 1932); Tide pool near Sabine Lake, (ML), one specimen.

Evorthodus Gill

E. lyricus (Girard)—Lyre Goby. Galveston, (Fowler, 1945); Aransas Bay, (Gunter, 1945).

Bollmannia Jordan

B. communis Ginsburg. Off Padre Island, (Ginsburg, 1942) ; Hildebrand (1954) found this species abundant offshore.

Microgobius Poey

M. gulosus (Girard)—Large-mouthed Goby. Aransas Pass and Corpus Christi, (Ginsburg, 1934) ; Mission Bay, (Baughman, 1950b) ; tide pool near Sabine Lake, (ML), one specimen.

M. thalassinus (Jordan and Gilbert). Aransas Pass, Harbor Island, and Corpus Christi. (Ginsburg, 1934) ; Galveston, (Fowler, 1945).

Gobiosoma Girard

G. bosci (Lacépède)—Naked Goby. Matagorda Bay and Corpus Christi, (Ginsburg. 1933) ; Copano and Aransas Bays, (Gunter, 1945).

G. robustum Ginsburg—Robust Goby. Corpus Christi, (Ginsburg, 1933).

Gobioides Lacépède

G. broussonneti Lacépède—Violet Goby. Freeport, (Baughman, 1950b), (ML) ; Sabine Lake (ML).

Bathygobius Bleeker

B. soporator (Valenciennes)—Mapo. Port Aransas Jetties, (Baughman, 1947).

SCORPAENIDAE—Scorpionfishes

Scorpaena Linnaeus

S. brasiliensis Cuvier. Galveston, (Gunter, 1948) ; Galveston, (Ginsburg, 1953).

S. calcarata Goode and Bean. Galveston, (Gunter, 1948) ; Port Aransas, (Baughman, 1950b) ; Texas, (Hildebrand, 1954) ; this is the commonest scorpaenid in waters of 8–35 fathoms according to Gunter (1948) and Ginsburg (1953).

S. dispar Longley and Hildebrand. Gulf, 45 fathoms, *Oregon* station 5 (Springer and Bullis, 1956). *S. similis* Gunter is a synonym.

S. plumieri Bloch. This is our commonest inshore scorpaenid; Ginsburg (1953) lists many records. *S. ginsburgi* Gunter is a synonym.

Pontinus Poey

P. longispinis Goode and Bean. Padre Island, (Ginsburg, 1953) ; Gulf, 95–175 fathoms, *Oregon* stations 1, 156, 1095, (Springer and Bullis, 1956).

Setarches Johnson

S. parmatus Goode. Padre Island, (Ginsburg, 1953) ; Gulf 200–300 fathoms, *Oregon* stations 541, 542, 1091, (Springer and Bullis, 1956).

TRIGLIDAE—Sea Robins

Both Ginsburg (1950) and Teague (1951) have revised *Prionotus;* the following is the nomenclature of Ginsburg (1950).

Prionotus Lacépède

P. martis Ginsburg. Off Sabine Pass, (Ginsburg, 1950).

P. ophryas Jordan and Swain. Galveston and Harbor Island, (Ginsburg, 1950) ; Texas, (Hildebrand, 1954).

P. paralatus Ginsburg. Apparently not uncommon in deep water. Galveston to Padre Island, (Ginsburg, 1950) ; Texas, (Hildebrand, 1954).

P. pectoralis Nichols and Breder. Aransas Pass, Corpus Christi Bay and Corpus Christi Pass, (Ginsburg, 1950) ; Texas, (Hildebrand, 1954).

P. roseus Jordan and Evermann. Off Matagorda Island, (Ginsburg, 1950).

P. rubio Jordan. Ginsburg (1950) states that this is the common triglid in the shallow northern Gulf; Hildebrand (1954) subsequently confirmed this.

P. scitulus Jordan and Gilbert—Slender Sea Robin. Aransas Bay, (Gunter, 1945); Corpus Christi, Shamrock Cove, Aransas Bay, Galveston Bay, (Ginsburg, 1950), as *P. s. latifrons* Ginsburg; (Hildebrand, 1954) ; not uncommon in bays.

P. stearnsi Jordan and Swain. Padre and Mustang Islands, Aransas Pass and Matagorda Peninsula, (Ginsburg, 1950) ; Texas, (Hildebrand, 1954).

P. tribulus (Cuvier)—Bighead Sea Robin*. Copano and Aransas Bays, (Gunter, 1945) ; off Corpus Christi Pass, Aransas Pass, Galveston and Aransas Bay, (Ginsburg, 1950), as *P. t. crassiceps* Ginsburg; Hildebrand (1954).

Bellator Jordan and Evermann

B. militaris (Goode and Bean)—Soldier Robin. Off St. Joseph's and Padre Island, (Ginsburg, 1950).

PERISTEDIIDAE

Peristedion Lacépède

P. gracile Goode and Bean. Gulf 55–300 fathoms, *Oregon* stations 7, 542, 550, (Springer and Bullis, 1956).

P. longispathum (Goode and Bean). Gulf 200–300 fathoms, *Oregon* stations 541, 542, 1091, (Springer and Bullis, 1956).

P. miniatum Goode. Gulf 125–300 fathoms, *Oregon* stations 162, 550, 1091, 1094, (Springer and Bullis, 1956). 27° 20′ N, 96° 20′ W, 100 fathoms, (ML), one specimen.

DACTYLOPTERIDAE

Dactylopterus Lacépède

D. volitans (Linnaeus)—Flying Gurnard. 15 fathoms SE of Port Aransas, (ML).

BOTHIDAE

Scopthalmus Rafinesque

S. aquosus (Mitchill). Galveston, (Baughman, 1950a).

Syacium Ranzani

S. gunteri Ginsburg. Gunter and Knapp (1951) and Hildebrand (1954) found this species abundant in the shallow Gulf.

S. papillosum (Linnaeus). Galveston and Corpus Christi, (Baughman, 1950a) ; shallow Gulf, (Gunter and Knapp, 1951).

Citharichthys Bleeker

C. cornutus (Günther). Gulf 103 fathoms, *Oregon* station 156, (Springer and Bullis, 1956).

C. macrops Dresel. SSE Aransas Pass, (Gunter, 1945) ; Freeport, Galveston, and Aransas Pass, (Baughman, 1950a) ; off Matagorda Island, (Hildebrand, 1954).

C. spilopterus Günther. This is the common bay and inshore member of this genus on the Texas coast.

Etropus Jordan and Gilbert

E. crossotus Jordan and Gilbert. Fairly common in shallow waters.

Engyophrys Jordan and Bollman

E. sentus Ginsburg. Texas Gulf, (Anderson and Lindner, 1941, Hildebrand, 1954).

Trichopsetta Gill

T. ventralis (Goode and Bean)—Texas, (Hildebrand, 1954) ; Gulf 23–220 fathoms, *Oregon* stations 2, 156, 158, 541, 1083, 1087, 1095, (Springer and Bullis, 1956).

Cyclopsetta Gill

C. chittendeni Bean. Common offshore according to Gunter and Knapp (1951) and Hildebrand (1954). Gunter (1946) described a new member of this genus *decussata*, from Texas. Hildebrand (1954) took specimens of *chittendeni* which approach the coloration of *decussata*, and he further states that this is probably a synonym.

C. fimbriata (Goode and Bean). Galveston, (Baughman, 1950a).

Poecilopsetta Günther

P. beani Goode. Gulf 160–300 fathoms, *Oregon* stations 164, 541, 542, 546, 1091, 1093, 1094, (Springer and Bullis, 1956).

PLEURONECTIDAE—Flounders

Paralichthys Girard

P. albiguttus Jordan and Gilbert—Gulf Flounder* (Sand Flounder). Uncommon on hard bottoms.

P. lethostigmus Jordan and Gilbert—Southern Flounder*. This is the common commercial flounder of the bays and shallow Gulf.

P. squamilentus Jordan and Gilbert. Ginsburg (1952c) states that this species is common from 80 to 120 fathoms.

P. triocellatus Miranda Ribeiro. Gulf, 18 fathoms, *Oregon* station 1086, (Springer and Bullis), (1956).

Ancylopsetta Gill

A. dilecta (Goode and Bean). Texas, (Baughman, 1950a) ; Gulf 31–49 fathoms, (Hildebrand, 1954) ; Gulf 50–103 fathoms, *Oregon* stations 2, 156, 158, (Springer and Bullis, 1956) ; apparently common in deep water.

A. quadrocellata Gill—Ocellated Fluke. Uncommon in bays, fairly common in the shallow Gulf.

ACHIRIDAE

Trinectes Rafinesque

T. maculatus (Bloch)—Hogchoker*. Not uncommon in bays; Gunter (1945) found this species to move offshore during the winter. Hubbs (1932) has established that this name has priority over *Achirus fasciatus* Lacépède, common in the literature. Some authors prefer to put this form in the genus *Achirus*.

Achirus Lacépède

A. lineatus (Linnaeus)—Striped Sole (Lined Sole). Not uncommon in bays and the Shallow Gulf. Records of *A. achirus* (Linnaeus) refer to this species.

Gymnachirus Kaup

G. texae (Gunter)—Naked Sole. Common in the shallow Gulf.

G. williamsoni (Gunter)—Naked Sole. South of Rockport, (Caldwell and Briggs, 1957).

CYNOGLOSSIDAE—Tonguefishes

Symphurus Rafinesque

S. civitatum Ginsburg. Off Aransas Pass and Galveston, (Ginsburg, 1951b); off St. Joseph's and Padre Island, Freeport and Sabine Bank, (Hildebrand, 1954).

S. diomedianus (Goode and Bean). Off Green's Bayou and Corpus Christi, (Hildebrand, 1954).

S. parvus Ginsburg. Gulf 18 fathoms, Oregon station 1086, (Springer and Bullis, 1956).

S. pelicanus Ginsburg. Off Padre Island, (Ginsburg, 1951b).

S. piger (Goode and Bean). Freeport, (Baughman, 1950a); Baughman's (op. cit.) record of *S. pusillus* (Goode and Bean) was probably this species.

S. plagiusa (Linnaeus)—Tonguefish. This is the common bay and inshore species of this genus on the Texas coast.

ECHENEIDAE—Remoras

Echeneis Linnaeus

E. naucrates Linnaeus—Remora*. This species is common as noted by Baughman (1950b).

Remilegia Gill

R. australis (Bennett)—Remora*. Off Corpus Christi, (Woods, 1942).

Remora Gill

R. remora (Linnaeus)—Remora* (Offshore Remora). There are specimens in the IMS collections, taken from sailfishes off Port Aransas.

Rhombochirus Gill

R. osteochir (Cuvier)—Remora* (Spearfish Remora). Off Port Aransas, (Springer and Hoese, 1958).

TRIACANTHIDAE

Triacanthodes Bleeker

T. lineatus Longley. Gulf 100–200 fathoms, *Oregon* stations 156, 541, 542, (Springer and Bullis, 1956).

BALISTIDAE—Triggerfishes

Balistes Linnaeus

B. capriscus Gmelin—Common Triggerfish*. Common on the snapper banks. Baughman (1950b) lists several records.

B. vetula Linnaeus—Queen Triggerfish*. Baughman (1950b) discusses the Texas occurrences of this species.

Canthidermis Swainson

C. maculatus (Bloch)—(Baughman, 1950b).

C. sobaco (Poey)—Ocean Triggerfish. Off Freeport, (Baughman, 1950b).

MONACANTHIDAE—Filefishes

Cantherines Swainson

Baughman (1950b) lists *C. pullus* (Ranzani) in the collections of the ML. There are four specimens inthese collections as *pullus*. Two are *Monacanthus hispidus* (Linnaeus) and two are *Balistes capriscus* Gmelin.

C. amphioxys (Cope). Gulf, *Oregon* station 1089, (Springer and Bullis, 1956).

Monacanthus Cuvier

M. hispidus (Linnaeus)—Common Filefish. Common, entering bays.

Alutera Cuvier

A. scripta (Osbeck)—Longtail Filefish* (Scrawled Filefish). Port Aransas, (Gunter and Knapp, 1951).

A. schoepfi (Walbaum)—Orange Filefish*. Common, entering bays.

OSTRACIIDAE—Trunkfishes

Reed (1941) lists *Lactophrys trigonus* from Texas. If it or *L. triqueter*, which Reed's specimen may have been, occur here they are uncommon. There are no specimens in collections to the writer's knowledge.

Lactophrys Swainson

L. tricornis (Linnaeus)—Cowfish*. Fairly common in the inshore Gulf, occasionally entering bays.

TETRAODONTIDAE—Puffers

Lagocephalus Swainson

L. laevigatus (Linnaeus)—Smooth Puffer*. Not uncommon, not known from bays.

Sphoeroides Lacépède

S. dorsalis Longley—Puffer*. 27° 29′ N, 96° 16′ W, (CNHM No. 45278) one specimen.

S. nephelus (Goode and Bean)—Puffer*. This is the common puffer of our coast. Gunter (1945), as *S. marmoratus* (Ranzani). This species has also been reported under the names *maculatus* and *spengleri*.

S. spengleri (Bloch)—Puffer*. Off Brazos Santiago. (Hildebrand, 1954).

S. testudineus (Linnaeus)—Puffer*. Galveston, (Baughman, 1950b).

Liosaccus Günther

L. cutaneus Günther. 27° 20′ N, 96° 18′ W, (CNHM) two specimens, (ML) one specimen.

DIODONTIDAE—Porcupine Fishes

Reed (1941) reports *Diodon hystrix* Linnaeus from Texas and Baughman (1950b) reports seeing one at Galveston. Apparently there are no specimens of this genus in collections.

Chilomycterus Bibron

C. schoepfi (Walbaum)—Burrfish* (Spiny Boxfish). Common, particularly in the bays during the summer.

MOLIDAE—Ocean Sunfishes

Mola Koelreuter

M. mola (Linnaeus)—Ocean Sunfish*. Off Cedar Bayou, (Baughman, 1950b), sight record; Corpus Christi Bay and Port Isabel, (Kemp, 1957).

GOBIESOCIDAE—Clingfishes

Gobiesox Lacépède

G. punctulatus (Poey). Texas, (Schultz, 1944); Texas, (Briggs, 1955).

G. strumosus Cope. This is the common clingfish of our coast. Baughman (1950b) lists several records as *Cotylus nigripinnis nigripinnis* Peters.

BATRACHOIDIDAE—Toadfishes

Opsanus Rafinesque

O. beta (Goode and Bean—Toadfish*. (Dogfish). This is the common toadfish of our coast, occurring in protected habitats.

Porichthys Girard

P. porosissimus (Valenciennes)—Midshipman. Common in the shallow Gulf, entering bays in the summer. Hubbs and Shultz (1939) place the Atlantic midshipman in a separate genus, *Nautopaedium* Jordan, on the basis of palatal dentition, but these differences are slight and not accepted as generic distinction by most authors.

LOPHIIDAE—Angler Fishes

Lophiomus Gill

L. sp.—Gulf Goosefish (Angler). See Springer and Hoese (1958) for a discussion of this species.

ANTENNARIIDAE—Frogfishes

Histrio Fischer

H. histrio (Linnaeus)—Sargassumfish*. This is the common species in *Sargassum;* records of *H. gibbus* (Mitchill) refer to this species.

Antennarius Lacépède

A. radiosus (Garman)—Frogfish. According to Hildebrand (1954) this is the common member of this genus in the western Gulf. Specimens in the collections of the ML reported by Baughman (1950b) as *A. pleuropthalmus* Gill seem to be the young of this species.

Phrynelox Whitley

P. nuttingi (Garman). 18 fathoms SE Port Aransas (Baughman, 1955) as *Antennarius nuttingi* Garman. 18 fathoms south of Port Aransas, 25 fathoms southwest of Port Aransas (ML).

P. scaber (Cuvier)—Frogfish*. Off Port Aransas, (Baughman, 1950b).

OGCOCEPHALIDAE—Batfishes

Halieutichthys Poey

H. aculeatus Mitchill. Woods (1942); Hildebrand (1954) took 510 specimens from 12 to 42 fathoms; specimens collected by McRae in the ML extend their bathymetric range to 100 fathoms.

Dibranchus Peters

D. atlanticus Peters. Gulf 29, 100, 400 fathoms, *Oregon* stations 540, 541, 542, 546, 548, 549, 550, 1087, (Springer and Bullis, 1956).

Ogcocephalus Fischer

There is considerable confusion concerning this genus in the Gulf and until a revision appears it seems wise to tentatively record the following two forms as understood by Longley and Hildebrand (1941).

O. cubifrons (Richardson)—According to Longley and Hildebrand (1941) this is the common inshore batfish in the western Gulf. Many are in collections as *O. vespertilio* (Linnaeus).

O. sp. A small, short-nosed batfish seems unidentifiable according to Hildrebrand (1954). There are specimens in the collections of the IMS as *O. parvus* (Longley and Hildebrand).

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Food Habits of Fishes and Larger Invertebrates of Lake Pontchartrain, Louisiana, an Estuarine Community

REZNEAT M. DARNELL

Department of Biology, Marquette University, Milwaukee, Wisconsin

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Introduction

During recent years the study of quantitative aspects of community metabolism has occupied the attention of increasing numbers of aquatic ecologists. As pointed out by Lindeman (1942), Ivlev (1945), Macfadyen (1948), Teal (1957) and others, rates of turnover in community metabolism are more satisfactorily expressed in terms of energy than in terms of biomass. Accordingly, a number of important studies have recently appeared dealing with quantitative aspects of the energy transfer associated with primary production in aquatic communities. Studies of the energetics involved in secondary production within restricted communities (Teal, 1957) also have provided valuable information. However, few attempts have been made to quantify the energy relations involved in secondary production in more complex aquatic communities, and these have not, in the opinion of the writer, been as rewarding. This lack of success has been occasioned largely by the tendency of the workers to greatly oversimplify pathways of exchange of nutrients and energy among the consumer organisms.

The concept of consumer "levels" as employed by Lindeman (1942) and others has

been justly and severely criticized by Ivlev (1945). Peterson and Jensen as early as 1911 stressed that the subdivision of animals into predators, detritus feeders, etc., must be treated with care since, "the boundaries are very often deleted in nature." Although, as suggested by Ivlev, some simplification may often be justified and necessary, such action should be based upon a thorough knowledge of the pathways of nutrient and energy transformation for the particular body of water. Computations regarding energy transfer resulting in secondary production should be preceded by adequate food analyses.

The study of the food habits of the Lake Pontchartrain inhabitants is based upon the above considerations and is intended as a first step toward the quantitative evaluation of the metabolic relations of the complex estuarine community. Whereas consideration of the food relations may carry certain value, practical and otherwise, intrinsic to each particular species, in aggregate this knowledge should also provide a reasonably detailed picture of the overall trophic processes of the community.

The present report embraces one aspect of an ecological survey of Lake Pontchartrain and adjacent waters of southeastern Louisiana. The physical environment and ecological aspects of the plankton, invertebrate, and fish populations will be published elsewhere. The organization of this survey and general sampling procedures have already been reported (Darnell, 1954). Research reports submitted to the State of Louisiana (Suttkus, Darnell, and Darnell, 1953, 1954, 1955, a-j) have included numerical aspects of the fish and invertebrate collections. All species of fishes listed in these reports as comprising at least one percent of the overall trawl and seine catches were included in the food studies, except three small, mainly shallow water species *(Cyprinodon v. variegatus, Fundulus grandis,* and *Syngnathus scovelli)*. In addition, a number of species of fishes were included for food analyses which were especially important seasonally or locally, or species which, because of size, speed, or maneuverability, were judged to be more abundant than the collections might indicate. Several of the most important species of large invertebrates were also included.

In carrying out the present study 1,399 detailed quantitative analyses and about 100 qualitative analyses were carried out on specimens representing 35 of the most important estuarine species. Nearly all specimens were collected by the writer within a 14 month period (July 1953–August 1954), providing a reasonably instantaneous picture of the community. Species for which the analyses were most complete include the southern bay anchovy, channel catfish, silverside, sand trout, speckled trout, spot, Atlantic croaker, pinfish, and blue crab. Due to lack of specimens and time, the analyses of the remaining species were incomplete in various degrees, representing a regrettable shortcoming in the present data. From the community standpoint this incompleteness is most serious for the very abundant gulf menhaden. For a single species, the stingaree, no specimens were examined. However, this fish was considered to be of sufficient importance in the community for inclusion of its food habits as reported in the literature.

Since the fishes and invertebrates which frequent the brackish-water estuary are derived from a variety of habitats, the published information regarding their food and general ecological relations is widely scattered, and an effort has been made herein to bring together this pertinent literature. Altogether the food relations of the fishes and invertebrates of the estuaries of eastern North America are still poorly known.

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Methods

Specimens for food analysis were collected by trawls and seines and were preserved shortly after capture. Habitat notes and measurements of the environmental factors are summarized briefly in the following section. An early effort was made to neutralize the contents and inhibit enzyme activity in the stomachs of the more carnivorous species by injection of alkaline formalin (borax solution) into the lumen shortly after capture. This proved ineffective, however, and was abandoned. Reference collections of plankton, nekton, and benthic food organisms were identified by specialists, and considerable attention was devoted to the proper taxonomic verification of the food species.

Laboratory food analyses were carried out entirely by the author or under his supervision according to the following procedure. Stomach contents were examined and the items sorted and identified. The percent fullness of each stomach was estimated, and the percentage volume of each type of food item in each stomach was determined (by volumetric displacement, in the case of the larger items, or by estimation against a grid painted below the analysis dish, in the case of the smaller, and more amorphic materials). Thus, for a given group of stomachs, not only is the often misleading "*percentage of tracts containing each item*" known ("*percent frequency of occurrence*" of authors), but also the more informative "*average percent of total stomach volume*". Intestinal contents were examined qualitatively to reveal any types of food items not encountered in the stomachs, and the percent fullness of the intestines was also estimated. Qualitative analysis of the intestines proved quite rewarding and should be incorporated

as standard procedure in future food studies. Body length, collecting and preserving data, sex (as determined by microscopic analysis of the gonads), and other pertinent information were recorded on the form data cards. Future studies of this type and magnitude should unquestionably employ keysort or I.B.M. cards to facilitate handling of data and correlation of variables.

Summarized results of the food studies were plotted by size group in traditional bar d'agrams. Where data were especially complete individual food items were lumped into major food categories, and the results plotted on semilog paper as frequency polygons depicting the average ontogenetic food changes of the particular species population. The log plot was employed because it was observed that ontogenetic food changes occurred most rapidly in the smallest size classes. When graphed in this manner, many of the ontogenetic food changes approach linearity.

General Description of Lake Pontchartrain

The geological history of the Lake Pontchartrain basin has been discussed by Russell (1936, 1938, 1940), Steinmeyer (1939), Fisk (1944, 1947a, b), and Gunter (1952). As indicated by these authors, the present Lake Pontchartrain represents a remnant of an arm of the Gulf of Mexico which was impounded by deltaic deposits of the Mississippi River around 2,000 years ago. Underlying sediments reveal a subsequent history of rapid filling chiefly by deposition of enormous quantities of silt and clay from overflow waters of the Mississippi River. Other streams and bayous have added smaller amounts of sandy sediments, and subaqueous tidal deltas have been deposited near the mouths of fresh and salt-water passes. Also active in filling the depression has been the persistent encroachment by marginal marsh and swamp. Wave dissection of such vegetation has resulted in rounding of shore contours and offshore deposition of great quantities of humus. This erosion is current and appears to have been most pronounced during hurricanes. Active subsidence of the lake bottom has partly counteracted these forces of deposition. Associated with the above processes a gradual freshening of the environment has taken place, and the area which some 5,000 years ago was characterized by marine species of *Venus, Pecten, Dosinia,* etc., and later by *Crassostrea virginica* and *Thais* spp., now forms habitat for large populations of *Rangia cuneata* and certain freshwater species.

Physiographically Lake Pontchartrain contains 635 square miles of surface area with a shoreline of about 100 miles. The average depth is around 11 feet, and except for a number of artificial dredge holes near the south shore which may exceed 30 feet, the maximum depth of the lake proper is 18 feet. The bottom of Lake Pontchartrain is characterized by gradual sloping although the only extensive stretches of shallow water, *i.e.* less than 6 feet, are found in the relatively infertile western sector.

During the period of the survey (July 1953-May 1955) the temperature of the open waters of Lake Pontchartrain ranged from a minimum of 9°C. in December to 34°C. in June and August. Shallow water temperatures often were higher, however, ranging up to 39°C. Winter temperatures were low and seldom exceeded 17°C., whereas the summer temperatures generally remained above 30°C. During the spring and fall an average monthly rate of change of about 5°C. was observed with the most rapid rise in April

or May and the most rapid drop in early November. Extensive species migrations were found to coincide with marked temperature changes, especially in the fall, and temperature is undoubtedly one of several important factors regulating such movements. No outstanding differences were observed between the temperatures of the various parts of the lake.

The salinity of Lake Pontchartrain during the period of study varied from 1.2 *per mille* after a heavy January rainfall to 18.6 *per mille* following influx of Gulf water in the wake of a September storm. The average salinity for most months, however, was less than 6 *per mille* and the maximum for most months was less than 9 *per mille*. The effect of addition of large quantities of fresh water (through rainfall and flooding) or salt water (through Gulf storms) was apparent for several months following the event. Marked differences in salinity from one part of the lake to another was obvious, and one month a salinity difference of 12.4 *per mille* was noted between different stations. In general, the freshest areas of the lake were found in the west and northwest sectors near the openings of the freshwater streams and passes, and the most saline areas in the eastern sector, especially near the mouths of the salt-water passes.

Stratification of the lake waters was not carefully investigated, although it was occasionally observed. As indicated by other workers, in warm water only a slight temperature differential is required to create density differences sufficient for stratification. In brackish waters such temperature-related density differences may often be reinforced by differences in salinity. This situation often manifests itself in the summer months, when a relatively cool wedge of salt water creeps in from the Gulf under the warmer and fresher lake waters. The importance of such salt water currents in facilitating the inward migration of Gulf-spawned larval fishes and invertebrates has been suggested by previous workers.

One of the most characteristic features of Lake Pontchartrain is the exceptionally high turbidity which imparts a chocolate appearance to the waters. The average summer Secchi disc visibility was about 6 feet, and rarely, on calm clear summer days the bottom was visible in 14 feet of water. During the remaining months, however, the visibility was lower, averaging only 2–3 feet the first winter. The turbid condition of the water was directly related to wind action which disturbed and raised bottom sediments even in the deepest portions of this shallow body of water. The most turbid portions of the lake appeared to be the shallowest waters, especially near the south shore, and in times of heavy wind and wave action Secchi disc readings of less than one inch were recorded for this disturbed area. The overall average of the Secchi disc readings for the total period of study was about 4 feet indicative of a highly and persistently turbid situation. Even this figure represents an understatement since on numerous occasions collecting trips were cancelled due to the stormy condition of the lake.

The plankton and the marsh and swamp vegetation bordering Lake Pontchartrain are discussed later in relation to the general nutrition of the community. It might be pointed out here that most of the fishes and larger invertebrates found in the lake are transients which normally spend only a portion of their life histories within the confines of the estuary. The marine species are most conspicuously represented by immature stages, whereas generally more mature individuals of the freshwater species are found in the lake.

Trophic Relations of Fishes and Invertebrates

Fishes

Carcharhinidae

Carcharhinus leucas (Müller and Henle). Bull Shark

The food habits of the bull shark have recently been discussed by Baughman and Springer (1950) who reviewed the works of Linton (1904), Nichols (1917), and Bell and Nichols (1921). These authors found the shark to be highly carnivorous although of somewhat indiscriminate taste. Food included fishes (sting rays, other sharks, shad and mackerel), the fin of a porpoise, crabs, echinoderm plates, and some vegetable fibers.

The stomachs of three bull sharks from Lake Pontchartrain were examined, and only two contained recognizable food. One specimen (780 mm.) had consumed a single large striped mullet *(Mugil cephalus)* (255 mm.) almost one third of its own body length. The second shark (805 mm.) contained within its stomach ten small menhaden *(Brevoortia patronus)* (66–103 mm.), a croaker *(Micropogon undulatus)* (67 mm.), a single white shrimp *(Penaeus setiferus)* and a small crab (probably *Callinectes sapidus)*. Fishes made up over 90 percent of the food encountered in both sharks.

A number of sharks, ranging in length up to around 7 feet, were encountered in the shallows as well as the deeper offshore waters of the lake. These are most probably referable to the species *C. leucas*. On one occasion the carcass of a large black drum (*Pogonias cromis*) was found floating at the surface a few miles from the southwest shore, and at the approach of the boat a single large shark and two smaller individuals abandoned the remains. When retrieved, the drum was found to have been severed cleanly in two just behind the anus, the remaining anterior half weighing 35 lbs. It was assumed that this drum was attacked by one of the sharks while the drum was feeding upon bottom mollusks, standing vertically in the water as is the habit of this species (see the section on *Pogonias cromis*). A number of alleged shark attacks upon bathers at Pontchartrain Beach (New Orleans) in the summer of 1953 may possibly be attributable to this species.

In the Lake Pontchartrain community *C. leucas* must be considered one of the top predators in the shallow as well as the deeper waters since it is one of the largest and most carnivorous of the predatory species. Its influence upon both the fish and invertebrate populations appears to be limited only by the relative scarcity of the species during most of the year.

Dasyatidae

Dasyatis sabina (Le Sueur). Stingaree

The food of stingarees has received only minor attention in the literature. Linton (1904), Hildebrand and Schroeder (1928), Gunter (1945), and McLane (1948) have reported the stomach content of stingarees to consist primarily of bottom-living invertebrates including clams, snails, annelids, amphipods, schizopods, mud crabs, sea urchin parts and fish bones, eye lenses, and sand.

No specimens from Lake Pontchartrain were examined although it may be assumed that in the lake the primary foods would be such small bottom invertebrates as clams

(*Rangia cuneata*), mud crabs (*Rithropanopeus harrisii*), and small blue crabs (*Callinectes sapidus*), supplemented with small shrimp, chironomid larvae, and annelids. A single cow-nosed ray (*Rhinoptera bonasus*) from Lake Pontchartrain examined in the field was packed with the bodies of small clams.

Lepisosteidae

Lepisosteus osseus oxyurus Rafinesque. Northern Longnose Gar

Food habits of the longnose gar have received attention by Forbes (1888), Mark (1890), Pearse (1918), Forbes and Richardson (1920), Evermann and Clark (1920), Hubbs (1921), Rimsky-Korsakoff (1930), Lagler and Hubbs (1940), Bonham (1941), Frisby (1942), and by Lagler, Obrecht, and Harry (1942) who summarized the work of earlier investigators. Published information indicates that the longnose gar feeds chiefly upon entomostraca and insect larvae until around 50 mm. (two inches) in length. At about this size it changes to a diet of fishes which then predominate in the food of the larger size groups. Depending upon the size of gar and upon the food available this fish has been reported to feed upon a variety of minnows, darters, silversides, and mosquitofish, as well as mullet, gizzard shad, smelt, suckers, bullheads, catfish, pike, killifish, perch, bluegills, rock bass, largemouth bass, and crappies. Crayfish, grass shrimp, and other invertebrates also have been noted in the stomachs of this fish. More recently McLane (1948) reported that longnose gar in Florida consume large numbers of threadfin shad (*Signalosa petenensis vanhyningi*) when these are available.

In the present study eight longnose gars (706–1180 mm.) from Lake Pontchartrain were examined, but only four contained food. About 98 percent of this material was made up of small fishes, with miscellaneous invertebrates and other items constituting two percent. One third of the fishes eaten were menhaden (*Brevoortia patronus*), and as many as three were encountered within one stomach. A single sea catfish (*Galeichthys felis*), about 100 mm. in length, also made up about one third of the volume of fishes consumed. Additional fish remains were probably bigeye herring (*Elops saurus*). Miscellaneous material included clams (*Rangia cuneata*), crabs, insects (Coleoptera, Diptera), and bits of undetermined organic material and detritus. The longnose gar is one of the top shallow water fish predators of the Lake Pontchartrain community.

Lepisosteus productus Cope. Spotted Gar

The food habits of the spotted gar in fresh water have been studied by Parker (1939), Bonham (1941), and Lagler, Obrecht, and Harry (1942). These authors have noted that fishes form the principal food of the adults, constituting up to 95 percent of the ingested material in some cases. Fishes consumed included gizzard shad (perhaps, the most important food), suckers, minnows, bullheads, pickerel, bluegills, round sunfish, black crappie, white crappie, largemouth bass, and yellow bass. When available large numbers of crayfish are consumed, as well as some grass shrimp and aquatic insects.

Food of the spotted gar in brackish water has been mentioned by Gunter (1945) and Lambou (1952, 1956). Gunter *(op. cit.)* cited a single unidentifiable fish from the stomach of a spotted gar taken from Copano Bay, Texas. Lambou *(op. cit.)*, however, found that in the brackish coastal marshes of southeastern Louisiana the species consumed blue crabs and fishes (primarily sunfishes) in about equal percentages.

Hunt (1953) discussed the food habits and community relations of the closely related

L. platyrhinchus from the Tamiami canal of southern Florida. In his study fishes made up 76 percent of the food of the gars, and the remainder consisted of invertebrates (snails, entomostraca, *Palaemonetes* sp., and insects). Fishes included the mosquitofish, killifish, molly, bluegill, spotted sunfish, and young warmouth bass.

Nine specimens of the spotted gar (405–555 mm.) from Lake Pontchartrain were examined, only seven of which contained food. This material consisted chiefly of crabs (70 percent) and fish (24 percent) with a small amount of miscellaneous material (6 percent). Crabs included the blue crab *(Callinectes sapidus)* which varied from 75 to 140 mm. in carapace width, surprisingly large for the size of the gars consuming them. At least some of the fishes consumed were clupeids, probably *Signalosa petenensis.* Included among the miscellaneous items were clam fragments *(Rangia cuneata)*, insects (Odonata), and undetermined organic material and detritus. In the Lake Pontchartrain community the spotted gar appears to feed more upon shallow water invertebrates than does the longnose gar, although small fishes are also taken.

Parker (1939) concluded that the spotted gar feeds mainly in the early morning hours, although Lambou (1952) indicated that most active feeding probably takes place in late evening or at night. Hunt (1953) was unable to distinguish any periodicity in feeding of the Florida spotted gars during the daylight hours.

Lepisosteus spatula Lacépède. Alligator Gar

A number of workers have referred to the food of the alligator gar in fresh and brackish waters, but no detailed systematic study of the food habits of this important species seems to have been reported. Jordan (1905) indicated that the alligator gar is a scavenger around piers in Pensacola, Florida, vying with sharks for garbage, and Viosca (as reported by Weed, 1923) concluded that the species is almost strictly a scavenger. A number of workers, however, have referred to the predatory habits of the species. Wortman (1882) considered the alligator gar to be a predator. Hussakof (1914) mentioned a large crappie and a short-nosed gar taken from stomachs of this fish, and Hildebrand and Towers (1927) listed large fish among the food of this species in Mississippi. Gowanloch (1940) listed fish and crabs among the food of Louisiana specimens. Bonham (1941) recovered an eel, a buffalo fish, and what appeared to be a sheephead from alligator gars taken in Texas, and Raney (1942) added that Texas specimens also consume large birds including ducks and water turkeys. Gunter (1945) found that 12 large alligator gars (600–1590 mm.) from the brackish waters of Copano Bay, Texas contained 13 fish, all of which appeared to be *Mugil cephalus.* Lambou (1952, 1956) studied the food of 30 alligator gars taken from the brackish marshes adjoining the northeastern shore of Lake Pontchartrain, Louisiana. Small blue crabs made up about 87 percent of the food, and fishes, shrimp, and undetermined material made up from three to four percent each. Lambou concluded that active feeding occurs late in the evening and possibly at night and in the morning.

In the present study, five specimens of alligator gar (903–1472 mm.) were examined in the laboratory, of which only three contained food. This material included 65 percent large blue crabs *(Callinectes sapidus)* and 35 percent striped mullet *(Mugil cephalus)*, as well as traces of clams *(Rangia cuneata)*, vegetation, undetermined organic material, and detritus. In addition to the above analyses, the stomachs of a large number of alligator gars were examined qualitatively in the field, and these were all found to be loaded with medium-sized and adult blue crabs. On a number of occasions these large predatory fish were observed feeding upon the extensive schools of adult striped mullet which

congregate along the north shore of Lake Pontchartrain in early fall. Active feeding was apparent both in the morning and in the afternoon. Large alligator gars were sometimes seen at the surface of deeper offshore waters of the lake. Hence they must be predators of deper, as well as shallow waters.

Whereas some scavenging undoubtedly does take place, the above studies leave little doubt regarding the predatory nature of this fish. In brackish coastal waters such as Lake Pontchartrain the primary foods of the species include the blue crab and the striped mullet, both of which are available in quantity in the shallow marshes and margins of the lake, as well as in the deeper waters.

Elopidae

Elops saurus Linnaeus. Bigeye Herring, Tenpounder

As a group the tenpounders are known to be generally carnivorous. Linton (1904) recorded six large penaeid shrimp from the stomach of a single specimen of *E. saurus* from Chesapeake Bay. Gunter (1945) reported that three out of five Texas specimens examined contained food including penaeid shrimp *(P. setiferus)* and two pinfish *(Lagodon rhomboides)*. McLane (1948) stated that in the St. Johns River of Florida the bigeye herring consumes large numbers of shad *(Signalosa petenensis vanhyningi)*. Knapp (1949) examined the stomachs of 156 specimens from the Texas coast and found shrimp in 76 percent, fishes in 34 percent, and crabs, squids, and other invertebrates in less than three percent each. Reid (1954) encountered only unidentifiable fish remains in the stomachs of Florida specimens. The same author (Reid, 1955a) analyzed eight bigeye herring (82–185 mm.) from northern Texas and found fishes (including clupeids and atherinids) in the stomachs of five individuals and small penaeid shrimp in the stomachs of four. A single stomach was empty. Dill and Woodhull (1942) mentioned that the related *E. affinis* in the Salton Sea, California, consumes desert minnows and beetles, and Hiatt (1947a) pointed out that in Hawaiian fishponds the congener, *E. machnata*, feeds primarily upon small fishes *(Gambusia affinis* and *Mollienesia latipinna)* with smaller quantities of crustaceans *(Leander debilis* and amphipods) and traces of snail shells.

Stomach contents of 16 bigeye herring (161–280 mm.) from Lake Pontchartrain were examined, although only five contained recognizable food. Fishes comprised the bulk (82 percent) of this material and included the anchovy *(Anchoa mitchilli diaphana)* (70 percent) and other unidentifiable fish remains (12 percent). Penaeid shrimp made up ten percent of the food and undetermined organic matter, eight percent. The presence of occasional strands of filamentous green algae (*Cladophora* sp.) indicated that foraging had probably taken place in the shallow margins of the lake.

Evidence from the south Atlantic and Gulf coasts points to the fact that *E. saurus* is an important shallow water predator, and within the size range 82–280 mm. it consumes quantities of small fishes and penaeid shrimp. Detailed study of the food of the different size groups would probably indicate food habits very similar to those of the speckled trout (*Cynoscion nebulosus*) of comparable lengths.

Clupeidae

Brevoortia patronus Goode. Gulf Menhaden

A number of workers have discussed the food of the several species of menhaden inhabiting the south Atlantic and Gulf coasts of the United States, and opinions regarding

the origin and nature of this food material have been divided among those who have held the species to be mud- or "ooze"-feeders and those who have considered the species to be plankton-strainers. Verrill (1871) reported that stomachs and intestines of menhaden (*B. tyrannus*) taken from the shallow coastal waters of New Jersey invariably were filled with the soft, "oozy" mud, containing a large proportion of organic matter such as abounds in the quiet parts of coastal bays, and he concluded that the menhaden obtains its nutriment, "by swallowing the mud and digesting the organic particles obtained in it". Goode (1879) examined the digestive tracts of about 100 menhaden (mostly *B. tyrannus*) taken from estuaries, rivers, and harbors along the Atlantic and Gulf coasts and also obtained the opinions of many commercial fishermen regarding the food of the species. On this basis, he stated, ". . . the plain inference seems to be that the food of the menhaden, in part at least, is the sediment which gathers upon the bottom of still, protected bays, which is largely composed of organic matter, and upon the vegetation which grows in such water." Goode presented further observations suggesting that the menhaden might also strain plankton from near-shore and marine waters. Linton (1904) reported the results of food studies of five menhaden (*B. tyrannus*) from North Carolina which seem to lend support to the notion of bottom feeding advanced by the above workers. Whereas the alimentary tracts of four of the menhaden were "packed with many kinds of copepods", the alimentary canal of the remaining fish was filled with greenish mud consisting of sand and vegetable debris together with diatoms and many kinds of algae, abundant foraminifera, numerous spines and spicules, and a small copepod fragment.

In describing the remarkable branchial filtering apparatus of the Atlantic menhaden, Peck (1894) pointed out the close resemblance between the microscopic appearances of the stomach contents and of plankton articially filtered from the surface waters at the time of capture, thus demonstrating rather conclusively that the menhaden does filter plankton from surface waters. He found that diatoms and dinoflagellates were especially abundant and that filamentous algae, copepods, a number of ciliate protozoans, and certain other small invertebrates were sometimes taken in quantity. In addition, large amounts of disintegrating organic matter from a variety of sources were consistently present, and varying quantities of "amorphous matter", which he assumed to be masses of bacteria, were noted to occur. Tintinnids were occasionally present in greater concentration in the food than in the surface water samples, however, suggesting that the menhaden might filter materials from subsurface waters as well. Bigelow and Schroeder (1953) described the feeding behavior of the species, and summarizing the work of Peck (*op. cit.*) they emphasized the mechanical nature of the straining action. Although no apparent voluntary selection takes place, larger animals are not consumed, and very small particles are not retained. Other writers including Gowanloch (1933), Gunter (1945), and Reid (1955a) have indicated that the related species of menhaden (*B. gunteri* and *B. patronus*) from the northern Gulf coast are also plankton-feeders, apparently basing their conclusions largely upon observation of surface-feeding schools.

In the present study 17 specimens of Gulf menhaden from Lake Pontchartrain were examined and all contained food material. In the five smallest individuals (38–48 mm.) the contents of both the cardiac and pyloric portions of the stomach were examined. Food of these small menhaden consisted chiefly of phytoplankton (82 percent), with small amounts of zooplankton and plant fragments. Detritus constituted 11 percent of the total food material. The bulk of the phytoplankton was made up of several species

of *Anabaena* which together comprised 77 percent of the total food, whereas the remaining phytoplankton was composed of diatoms (*Coscinodiscus* sp., *Melosira* sp., *Nitzschia* sp., and *Synedra* sp.). Zooplankton included rotifers (*Keratella* sp. and *Trichocerca* sp.), as well as a few copepods. These small menhaden obviously had been straining plankton, and the presence of large quantities of *Anabaena* indicates that they were feeding at the surface on floating blooms of this phytoplankter, substantiating direct observations to this effect. It appears likely that these young fishes may also strain plankton at depths below the surface, although there is no direct evidence supporting such activity.

The 12 larger menhaden (85–103 mm.) were examined early in the study, and unfortunately, only the contents of the muscular pyloric region of the stomachs of these specimens were included for analysis. At least 99 percent of the material encountered appeared to be ground organic matter and silt, and a few occasional diatoms (*Coscinodiscus* sp.), foraminiferans, and copepods were also present. Although these larger menhaden can not be compared exactly with the smaller specimens, certain qualitative differences in the food of the two groups were suggested. During the field studies menhaden around 100 mm. in length were frequently captured in great abundance near the south shore of Lake Pontchartrain where wave action was reducing the organic material of the marshy shore to the consistency of coffee grounds. Here a suspension of ground up organic matter was almost always in evidence, and at times of heavy wave action (northerly winds) the water frequently displayed the physical appearance of black drawing ink (giving Secchi disc readings of less than one inch). The menhaden appeared to be thriving upon this suspended material, and the laboratory food analyses, while not proving the point, clearly substantiated this possibility. Phytoplankton was not the primary food of these larger menhaden since diatoms and other forms would have been recognizable, even if partially ground.

The conclusion reached on the basis of present knowledge is that the menhaden feeds by filtration. Although the primary food of the species seems to consist of planktonic algae and microcrustacea (suspended within the water), alternate food sources may be exploited when available. Surface scums of *Anabaena* enter the diet of the young. Likewise, suspended material other than living plankton (silt, mud, chopped and decaying bits of vegetation, bottom invertebrates, etc.) may be filtered from the water, suggesting falsely that the species had been feeding directly upon the bottom. Suspended bacteria which are undoubtedly ingested in some quantity may be considered as planktonic (Eddy, 1934). The real importance of each of these alternate food sources in the economy of the species remains to be determined, but from the foregoing it may be inferred that within turbid estuaries their combined importance may be considerable.*

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* In the spring and fall of some years the floating *Anabaena* scum is so abundant on Lake Pontchartrain that this phytoplankter literally forms mounds upon the surface of the water, and the fact that young menhaden are able to exploit this food source suggests that the numerical success of a particular young menhaden crop may be related to some extent, to the success of the *Anabaena*. In turn, the *Anabaena* crop (as indicated by unpublished quantitative plankton data) is most extensive during years of heavy rainfall when nutrient-rich waters drain from flooded marshes and swamps, maintaining relatively fresh conditions (less than 8‰) in the estuary. Under low salinity conditions, marine predators would tend to be less abundant, thus further enhancing the size of the young menhaden population. Suttkus (1956) has pointed out that spawning does not take place inside Lake Pontchartrain. Hence, in addition to the availability of food and predators, hydrographic conditions of a particular year, insofar as they affect transport of larvae, may also play a decisive role in determining the success of the new year-class.

Dorosoma cepedianum (Le Sueur). Gizzard Shad

The food of the gizzard shad in fresh waters has received the attention of a number of investigators including Forbes (1878, 1880a, 1888), Forbes and Richardson (1920), Tiffany (1920, 1921), Hildebrand and Towers (1927), Ewers and Boesel (1936), Kuhne (1939), Rice (1942), and Dendy (1946). These workers have pointed out that young gizzard shad feed primarily upon planktonic crustaceans, minute algae, and insect larvae whereas adults consume chiefly vegetable debris and mud from the bottom supplemented by a variety of forms including planktonic protozoa, rotifers, crustaceans, and small fishes, as well as a number of bottom invertebrates and algae. From the brackish waters of Chesapeake Bay, Hildebrand and Schroeder (1928) analyzed the food of 10 specimens. Vegetable debris comprised 80 percent of the material with sand and mud making up the bulk of the remainder. Miscellaneous items included three foraminiferans, a diatom, a difflugia, and a copepod.

Eleven specimens of adult gizzard shad (101–278 mm.) from Lake Pontchartrain were examined. Although all specimens contained some food material, this substance was found to be recognizable only before being subjected to the pulverizing action of the muscular pyloric portion of the stomach. Three primary types of material encountered in the digestive tracts included foraminifera, undetermined organic material and detritus, and silt, each of which made up over one-fourth of the total food volume. Eleven percent of the consumed material was sand, and traces of a variety of bottom invertebrates and plants made up the remainder. These included remains of sponges, snails, clams *(Rangia cuneata)*, annelids, ostracods, and copepods, as well as filamentous algae, seeds, and leaves of vascular plants. The Louisiana specimens undoubtedly had fed exclusively upon the surface of the bottom, and the presence of a high percentage of foraminifera and other invertebrates suggests that the shad exercised considerable selectivity in their bottom feeding.

Signalosa petenensis (Günther). Threadfin Shad

Apparently the food habits of the threadfin shad have not previously been reported, although McLane (1948) observed that in the St. Johns River of Florida where the species is very abundant it frequently swims with its mouth open, just breaking the surface of the water while feeding upon plankton. In the Lake Pontchartrain study the stomach contents of five specimens (69–103 mm.) were examined, only three of which contained recognizable food. Plankton made up 76 percent of the material, whereas detritus made up 14 percent, and sand 10 percent. Included among the plankton organisms were diatoms (31 percent), flagellates (including *Volvox* sp.) (19 percent), rotifers (including *Keratella gracilenta*) (18 percent), and copepods (8 percent). Recognizable amphipods were found in the intestines of one shad, although the intestines generally contained a mud-like material.

The threadfin shad, like young menhaden, appear to feed upon surface plankton, and this was borne out not only by food analysis but also by observations in Lake Pontchartrain of surface-feeding schools. The presence of amphipods, mud, and sand in the tracts of the Louisiana specimens, however, suggests that some feeding must take place near or upon the bottom.

ENGRAULIDAE

Anchoa mitchilli diaphana Hildebrand. Southern Bay Anchovy

Hildebrand and Schroeder (1928) analyzed the food of 44 specimens of *Anchoa m.*

mitchilli from Chesapeake Bay. The sole food of the young was found to be copepods, whereas the adults consumed both copepods and schizopods. In addition, cannibalism was indicated by the presence of two small anchovies in the food of the adults, and the occurrence of three small gastropods and an isopod indicated some bottom feeding. Reid (1954) mentioned that the food of anchovies from Cedar Key, Florida, is "small crustaceans of the class Malacostraca."

In the Lake Pontchartrain study micro-zooplankters, including rotifers and both cyclopoid and calanoid copepods, constituted an important portion of the diet of the smallest individuals (Table 1 and Fig. 1). With increase in size these forms were con-

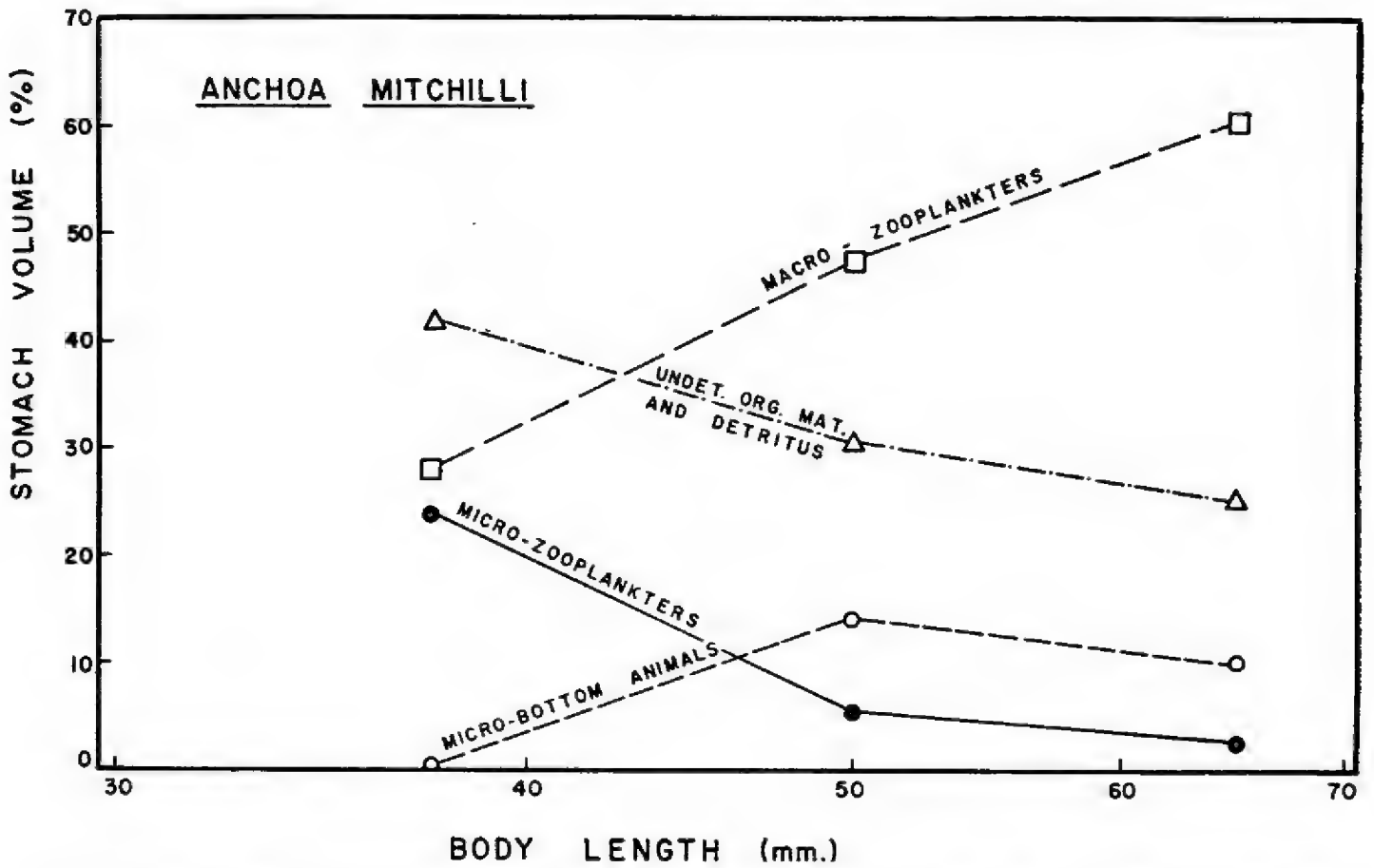

FIG. 1. Ontogenetic food progression of *Anchoa mitchilli*. (Body length refers to standard length.)

sumed less frequently, and in the largest anchovies they made up less than two percent of the food material. Undoubtedly, micro-zooplankton is also one of the chief sources of nutrition of anchovies smaller than 30 mm.

Remains of small shrimp and fishes made up a prominent portion of the food of anchovies of all sizes examined. These forms, somewhat loosely referred to as macro-zooplankton, constituted 28 percent of the material consumed by the smallest anchovies and increased to over 60 percent in the largest size class. Included in this food category are adult schizopods, larval and post-larval penaeid shrimp, larval fishes (including clupeids and probably some larval anchovies, again indicating cannibalism) and a single small naked goby *(Gobiosoma bosci)*.

Small bottom-dwelling mollusks and crustaceans were scarcely represented in the diet of the smallest anchovies. This material was conspicuous in the food of the two larger size classes, however, making up over ten percent of the food volume in both groups. Included among these micro-bottom animals were minute snails, clams *(Rangia cuneata)*, isopods, amphipods, ostracods, and harpacticoid copepods. The presence of such forms in the stomachs of the anchovies indicates that the species must feed to some extent upon the bottom since the mollusks and benthic microcrustaceans apparently are unavailable elsewhere. The micro-bottom animals, as well as small quantities of sand, were most

TABLE 1

Occurrence of food items in digestive tracts of 92 *Anchoa mitchilli*

FOOD ITEMS	30.0–44.0 mm. 15 examined 13 with food		45.0–49.0 mm. 25 examined 21 with food		50.0–54.0 mm. 22 examined 19 with food		55.0–59.0 mm. 19 examined 18 with food		60.0–74.0 mm. 11 examined 10 with food	
	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume
Rotifera	6.7	3.9	4.0	0.3	.....	.....	.....	.....	.....	.....
Ostracoda	.....	.....	4.0	0.8	.....	.....	5.3	T	.....	.....
Copepoda (undet.)	26.7	11.0	24.0	9.4	4.5	.....	21.1	1.5	.....	.....
Calanoid	26.7	9.0	16.0	1.4	4.5	T	21.1	3.5	27.3	0.5
Cyclopoid	.....	.....	.....	.....	4.5	0.5	.....	.....	.....	.....
Harpacticoid	6.7	0.3	12.0	0.4	13.6	3.3	.....	.....	9.1	1.3
Mysid shrimp	20.0	28.1	48.0	52.0	50.0	43.8	42.1	34.5	45.5	40.3
Isopoda	.....	.....	8.0	5.4	4.5	8.5	10.5	7.3	.....	.....
Amphipoda	.....	.....	16.0	6.0	9.9	1.2	10.5	2.6	.....	.....
Insecta	6.7	1.0	4.0	0.8	.....	.....	.....	.....	.....	.....
Mollusca										
Rangia cuneata	.....	.....	4.0	0.2	4.5	0.6	5.3	2.9	.....	.....
Gastropoda	.....	.....	4.0	2.3	.....	.....	15.8	3.4	9.1	2.7
Vertebrata										
Gobiosoma bosci	.....	.....	.....	.....	.....	.....	5.3	6.8	.....	.....
Fish larvae	.....	.....	.....	.....	.....	.....	5.3	7.3	9.1	13.4
Fish remains	.....	.....	.....	.....	.....	.....	.....	.....	27.3	19.3
Planktonic diatoms	.....	.....	4.0	0.4	.....	.....	.....	.....	.....	.....
Seeds	6.7	1.0	.....	.....	.....	.....	5.3	1.2	.....	.....
Eggs and cysts	13.3	3.2	4.0	T	4.5	0.2	5.3	0.5	.....	.....
Organic mat. (undet.)	73.3	34.7	48.0	6.9	68.2	33.7	68.4	22.8	72.7	19.2
Detritus	33.3	7.2	48.0	13.4	72.7	7.3	63.2	5.1	90.9	3.3
Sand	.....	.....	12.0	0.4	13.6	0.8	15.8	0.4	27.3	.....
SUMMARY										
Copepoda		20.3		11.2		3.8		5.0		1.8
Mysid shrimp		28.1		52.0		43.8		34.5		40.3
Isopoda and amphipoda		0.0		11.4		9.7		9.9		0.0
Fishes		0.0		0.0		0.0		14.1		32.7
Miscellaneous		9.1		4.8		0.8		8.0		2.7
Incidental and undet.		41.9		20.7		41.8		28.3		22.5

* Stomach and intestine included.

frequently encountered in the stomachs of anchovies taken during the winter and spring months suggesting that more intensive bottom-feeding may take place at these seasons of the year.

Undetermined organic material and detritus was most prominent in the food of the smallest size class (42 percent) and declined to one-fourth of the food volume of the largest fish. This substance was generally of fine particulate nature and appeared to be derived primarily by straining of suspended matter from the water rather than by scooping of surface material directly from the bottom. The decline in consumption of this detritus by the larger anchovies paralleled a decline in consumption of micro-zooplankters, as might be expected if straining were involved, and the great volumetric preponderance of this suspended detritus in the food of the young raises the trivial question of which should be considered "incidental", detritus or micro-zooplankton. The fact that the detritus was decreasing as the micro-bottom animals increased points to a greater degree of selectivity by the larger anchovies, and this, in turn, was related to the increased consumption of shrimp and fishes.

In summary, the Lake Pontchartrain anchovy population appears to pass through two ontogenetic feeding stages. Young individuals are plankton strainers and consume large quantities of micro-zooplankton and suspended detritus. The relative absence of phytoplankton suggests that such straining occurs near the bottom. With increasing size the species exercises greater selectivity, preying chiefly upon small shrimp and fishes and supplementing this diet with occasional bottom-dwelling mollusks and crustaceans. Detritus apparently forms an important nutritional supplement in both the young and adult.

In connection with his studies in East Bay, Texas, Reid (1955a, b) indicated that the abundance of the anchovy population depends "upon the mass of zooplankton". Whereas this may be the case for the Chesapeake Bay specimens of Hildebrand and Schroeder *(loc. cit.)*, it is only partially true for the Louisiana population which, as indicated, consumes copious quantities of detritic matter.

The daily pattern of feeding activity of the anchovy is not entirely clear. Examination of Figure 2 indicates that both the young and adults feed during the middle portion of the day, although the adults seem to commence feeding activities earlier in the morning than do the young.

Belonidae

Strongylura marina (Walbaum). Atlantic Needlefish

Hildebrand and Schroeder (1928) recorded the food of 18 specimens of needlefish. Seventeen had taken small fishes (*Mugil curema, Fundulus diaphana,* and silversides) while a single specimen had eaten shrimp. McLane (1948) reported that needlefish consume large numbers of shad *(Signalosa petenensis vanhyningi)* in the St. Johns River of Florida.

Seven specimens of the needlefish (357–457 mm.) from Lake Pontchartrain were examined, all of which contained food. Small fishes (*Anchoa mitchilli diaphana* and others) made up almost two-thirds of this material. Insects (adult Diptera and Coleoptera) and vegetation (*Cladophora* sp. and some vascular plant material) made up less than five percent. Almost one-third of the stomach content consisted of undetermined organic matter which appeared to be largely fishes and invertebrates in advanced stages of digestion.

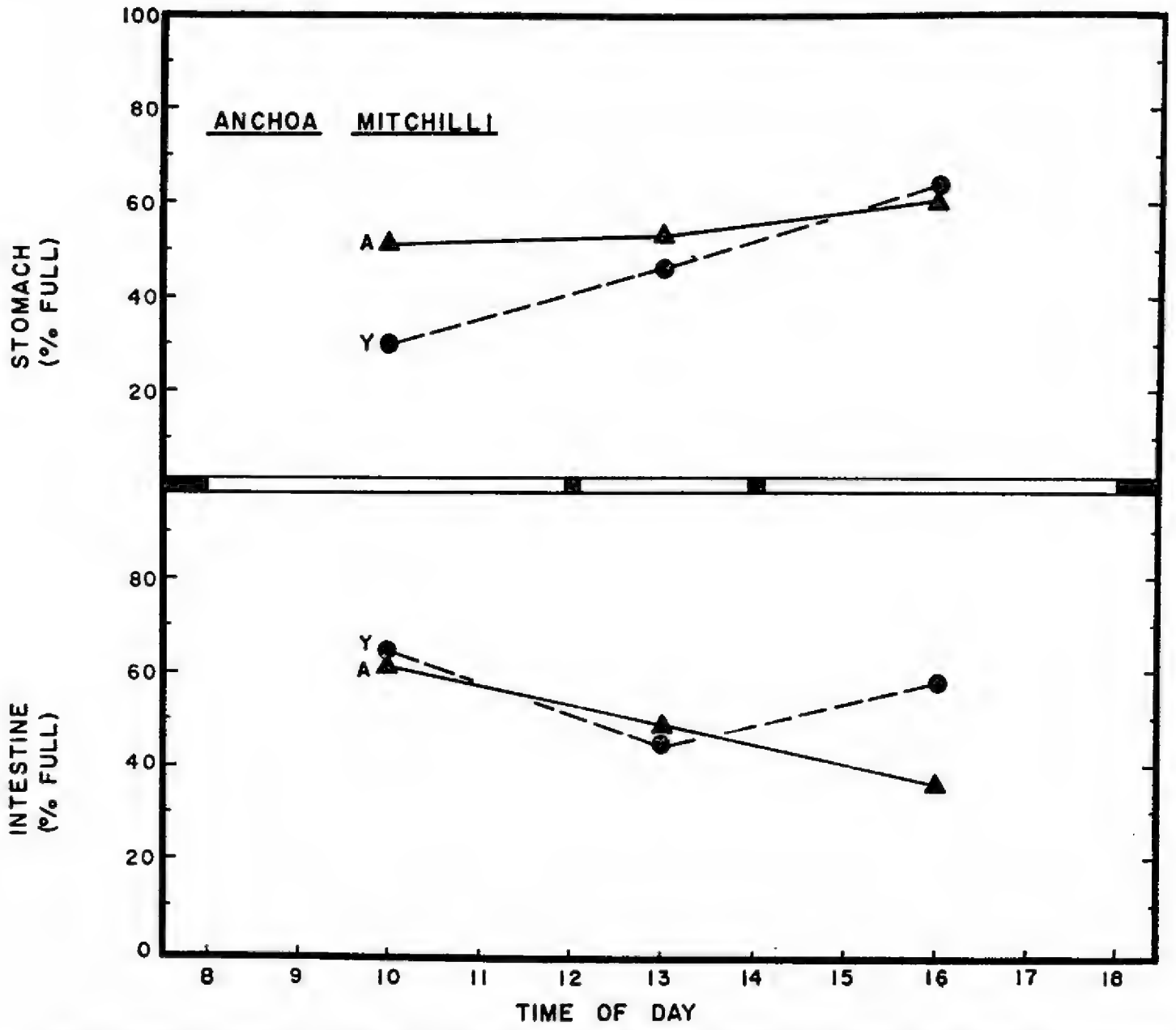

FIG. 2. Hourly pattern of percent-fullness of stomach and intestine of *Anchoa mitchilli* (young and adult).

The food habits of the needlefish are not well known. Within the size range studied, the species is a predator, feeding upon small fishes, insects, and crustaceans. This fish was frequently observed to be active near the surface in deeper water throughout the lake where it must feed on anchovies and young clupeids, although stomach analyses show that it does forage in the weedy shallows of Lake Pontchartrain.

ARIIDAE

Bagre marina (Mitchell). Gafftopsail Catfish

The food of adult gafftopsail catfishes has been reported by Gudger (1916), Gunter (1945), Knapp (1949), Reid (1955b), and Reid, Inglis, and Hoese (1956). These authors have shown that this fish feeds primarily upon blue crabs and penaeid shrimp, although fishes (including menhaden, worm eels, and other species), and various invertebrates (squids, small crabs, and insects) may also be taken. A single adult specimen from Lake Pontchartrain contained only unrecognizable material. Nothing is known of the food habits of small individuals.

Galeichthys felis (Linnaeus). Sea Catfish, Hardhead

Linton (1904) examined the food of 17 hardhead catfish from Chesapeake Bay and found clams (soft parts and valves), snails, annelids, amphipods, shrimp, sea urchin remains, and fish bones and eye lenses, as well as some sand. Smith (1907) indicated that

in North Carolina this fish is a bottom-loving species which feeds chiefly on worms and small crustaceans, but readily eats fish flesh or fowl, dead or alive. Perhaps, he had in mind the baits with which this catfish may be taken.

Gunter (1945) examined the stomach contents of 85 individuals from Texas of which 59 contained recognizable food. These fish ranged in size from 240 to 360 mm. except for one which was only 100 mm. in length. Blue crabs *(Callinectes sapidus)* and mud shrimps *(Callianassa jamaicense lousianensis)* made up about 90 percent of the food of these large catfishes, and Gunter *(op. cit.)* suggested that this fish can root soft-shelled crabs from hide-aways in the mud. Other identified material included penaeid shrimp *(P. aztecus)*, oyster crabs (*Panopeus* sp.), hermit crabs, a nudibranch, a small mullet, and a small sea catfish (indicating cannibalism). Fish bones and a clam shell were present, and although no specific mention was made of the presence of bottom detritus, indistinguishable material was noted in five stomachs. Knapp (1949) reported that of 468 hardhead catfish examined from the Texas coast, 87 percent had consumed shrimp, whereas fishes (including menhaden) appeared in about 14 percent, crabs in 6 percent, and squids and other invertebrates were present in less than one percent. Reid (1954) analyzed the food of five specimens from Florida. Four small individuals (91–116 mm.) contained many copepods as well as amphipods, mysids, polychaetes, and shrimp. One adult contained crabs, shrimp, and fishes. Reid (1955a) later reported on the examination of 14 specimens from northern Texas, of which 11 contained food. Six small individuals (82–91 mm.) had eaten "myriads" of copepods, some shrimp, and unidentified fish. Five larger catfishes (144–191 mm.) had consumed one xanthid crab, one fish, and quantities of "pelecypod debris".

Of the specimens examined from Lake Pontchartrain, smaller individuals had consumed quantities of small bottom-dwelling invertebrates (Table 2). These included amphipods (10 percent), mud crabs (16 percent), and chironomid larvae and pupae (13 percent), as well as smaller percentages of hydroids, clams, snails, harpacticoid copepods, schizopods, isopods, and water beetles. Bottom invertebrates were also prominent in the food of the larger sea catfishes, although these invertebrates tended to be somewhat larger in size and included higher percentages of both mud crabs and blue crabs. Adults consumed fewer amphipods, but the percentages of most other invertebrate groups remained relatively unchanged.

Fish remains consisting mainly of bones, scales, and lenses of eyes were present in the stomachs of catfishes of both size groups. Since no soft remains of fishes were encountered, however, it is assumed that no live fishes had been eaten and that the hard parts were strained from the surface of the bottom mud. These remains were least prominent in the stomachs of the adults indicating a greater apparent degree of selectivity within this group. Undetermined organic material and detritus constituted over one-third of the stomach contents in both sizes of sea catfish. This material which appeared to have been derived from the surface layer of the bottom deposits was more prominent in the diets of the young than of the adults.

The Lake Pontchartrain specimens indicate that within the size range investigated both young and adult sea catfish are bottom feeders which take in quantities of benthic invertebrates together with much bottom surface debris and detritus. Although little change was evident in the types of food consumed by the two size groups, the adults appeared to take in larger items, and especially more crabs. Increase in size appeared to be accompanied by somewhat greater selectivity involving a decrease in the consumption of both miscellaneous bottom materials and detritus.

TABLE 2

Occurrence of food items in digestive tracts of 40 *Galeichthys felis*

FOOD ITEMS	90.0–169.0 mm. 19 examined 19 with food		170.0–229.0 mm. 21 examined 17 with food	
	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume
Copepoda—Harpacticoid	5.2	.....	.....	.....
Mysid shrimp	10.5	1.9	4.8	1.3
Isopoda	42.1	1.8	23.8	2.1
Amphipoda	68.4	9.5	38.1	4.0
Palaemonidae	.....	.....	4.8	0.5
Crabs (undet.)	.....	.....	4.8	3.8
Rithropanopeus harrisii	47.4	15.7	61.9	27.8
Callinectes sapidus	.....	.....	9.5	2.3
Insecta (undet.)	5.2	0.1	.....	.....
Coleoptera	10.5	0.7	28.6	3.7
Diptera—larvae	89.5	10.6	61.9	10.3
Pupae, adults	26.3	2.0	14.3	0.6
Arachnida	....	.....	4.8	0.4
Mollusca				
Rangia cuneata	15.8	1.3	4.8	.....
Gastropoda	5.2	.....	4.8	.....
Hydroids	10.5	0.1	.....	.....
Vertebrata				
Fish remains	63.2	11.1	38.1	5.2
Vascular plants	10.5	.....	.....	.....
Organic mat. (undet.)	78.9	31.6	76.2	27.3
Detritus, Sand	68.4	13.6	81.0	10.8
SUMMARY				
Mysid shrimp		1.9		1.3
Isopoda, Amphipoda		11.3		6.1
Insecta		13.4		14.6
Crabs		15.7		33.9
Miscellaneous		12.5		6.1
Detritus, undet.		45.2		38.1

* Stomach and intestine included.

The total evidence available indicates that during its life history the sea catfish may actually pass through three feeding stages. Zooplankton, especially copepods, appears to be an important food for individuals less than 100 mm. in length. Above this size micro-bottom invertebrates assume importance, and these grade into larger crabs and fishes in "sea cats" above 200 mm. Much bottom detritus was noted in the Louisiana specimens, although this material has not been recorded as food for the species by workers in other areas.

ICTALURIDAE

Ictalurus furcatus (Le Sueur). Blue Catfish

The food of the blue catfish appears to have been largely neglected in the literature. Forbes (1888) found that a single specimen had eaten only fishes. Forbes and Richardson (1920) mentioned that fragments of bark, insect remains, and miscellaneous organic debris were also consumed and that blue catfish are caught on trot-lines baited with fishes and crayfish. Hildebrand and Towers (1927) reported a single small specimen (195 mm.) had fed on crustaceans, insects, fishes, and vegetation. Gunter (1945) found that four large blue catfish (280–305 mm.) from brackish waters of southern Texas had consumed grass shrimp (*Palaemontes* sp.), algae, and some indistinguishable material.

In the Lake Pontchartrain specimens of the smallest size group (60–129 mm.), zooplankton, including schizopods and calanoid copepods, constituted the most important single food, making up almost one-half of the stomach volume (Table 3 and Fig. 3). This material, however, was barely represented in the stomachs of the larger fish. Undoubtedly

TABLE 3

Occurrence of food items in digestive tracts of 78 *Ictalurus furcatus*

FOOD ITEMS	60.0–129.0 mm. 18 examined 15 with food		130.0–199.0 mm. 18 examined 16 with food		200.0–229.0 mm. 17 examined 15 with food		230.0–411.0 mm. 25 examined 23 with food	
	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume
Ostracoda	.....	.....	11.1	T	17.6	0.2	.....	.....
Copepoda								
Calanoid	5.6	12.6	.....	.....	.....	.....	.....	.....
Harpacticoid	.....	.....	11.1	0.5	.....	.....	.....	.....
Mysid shrimp	27.8	36.0	16.7	1.5	11.8	0.4	24.0	0.2
Isopoda	22.2	4.2	11.1	.....	23.5	0.4	16.0	4.8
Amphipoda	50.0	4.4	55.6	19.1	29.4	23.0	52.0	1.8
Palaemonetes sp.	.....	.....	.....	.....	5.9	.....	8.0	2.6
Macrobrachium ohione	.....	.....	.....	.....	.....	.....	4.0	1.0
Penaeus setiferus	.....	.....	.....	.....	.....	.....	4.0	2.6
Callianassa sp.	.....	.....	.....	.....	5.9	5.1	4.0	1.3
Crabs								
Rithropanopeus harrisii	.....	.....	44.4	10.9	47.1	2.4	20.0	6.4
Callinectes sapidus	5.6	.....	5.6	1.0	5.9	0.8	24.0	3.0
Insecta								
Coleoptera	16.7	1.7	33.3	0.3	29.4	0.5	8.0	..
Diptera	27.8	0.5	27.8	1.3	52.9	0.8	40.0	0.6
Hemiptera	.....	.....	5.6	.....	5.9	.....	.....	.....
Homoptera	.....	.....	.....	.....	.....	.....	4.0	.....
Hymenoptera	.....	.....	5.6	.....	11.8	.....	4.0	.....
Orthoptera	.....	.....	5.6	.....	5.9	.....	4.0	.....
Arachnida	.....	.....	.....	.....	5.9	.....	.....	.....
Annelida	5.6	.....	5.6	1.3	.....	.....	12.0	0.7
Mollusca								
Rangia cuneata	5.6	.....	72.2	25.3	76.5	36.0	52.0	9.9
Mytilopsis leucopheata	.....	.....	5.6	.....	23.5	6.7	16.0	2.1
Gastropoda	.....	.....	5.6	.....	35.3	0.5	4.0	.....
Hydroids	.....	.....	.....	.....	5.9	0.1	4.0	.....
Vertebrata								
Anchoa mitchilli	.....	.....	.....	.....	11.8	9.9	4.0	0.5
Citharichthys spilopterus	.....	.....	.....	.....	.....	.....	8.0	7.3
Menidia beryllina	.....	.....	.....	.....	.....	.....	4.0	0.4
Micropogon undulatus	.....	.....	.....	.....	5.9	0.7	12.0	8.3
Syngnathus sp.	.....	.....	.....	.....	.....	.....	4.0	0.4
Fish remains	.....	.....	11.1	3.5	11.8	2.3	24.0	13.5
Algae—filamentous	.....	..	5.6	3.3	.....	.....	32.0	25.7
Vascular plants	5.6	0.2	5.6	.....	5.9	.....	24.0	0.5
Eggs and cysts	.....	.....	5.6	.....	.....	.....	..	.....
Organic mat. (undet.)	88.9	26.3	66.7	25.5	76.5	10.1	52.0	3.3
Detritus	33.3	10.6	27.8	6.2	23.5	0.3	32.0	1.1
Sand and silt	11.1	3.8	16.7	0.4	17.6	0.1	40.0	2.3
SUMMARY								
Copepoda, Ostracoda, Mysids		48.6		2.0		0.6		0.2
Isopoda, Amphipoda		8.6		19.1		23.4		6.6
Macrocrustacea		0.0		11.9		8.3		16.9
Mollusks		0.0		25.3		43.2		12.0
Fishes		0.0		3.5		12.9		30.4
Vegetation		0.2		3.3		0.0		26.2
Misc. Invertebrates		2.2		2.9		1.4		1.3
Incidental and Undet.		40.7		32.1		10.5		6.7

* Stomach and intestine included.

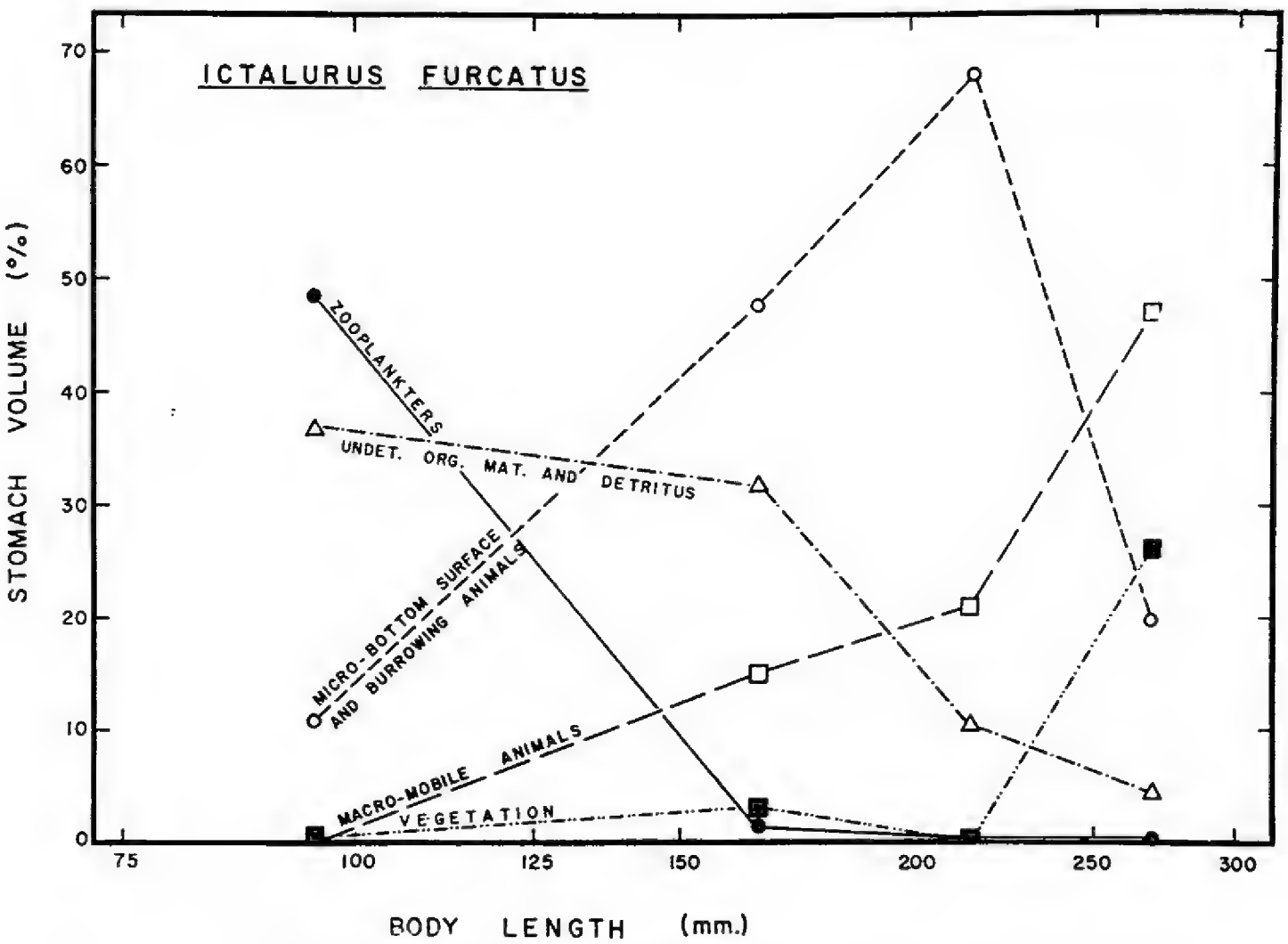

FIG. 3. Ontogenetic food progression of *Ictalurus furcatus*.

zooplankton also constitutes a major portion of the diet of fishes smaller than 60 mm.

Small bottom animals, including surface as well as burrowing forms, made up 11 percent of the food of the smallest size class. This material increased in the intermediate size classes, reaching a peak of consumption in the 200–229 mm. blue catfish where it constituted over two-thirds of the total food. In the largest size class this material declined, however, to one-fifth of the volume of the material consumed. Included among these bottom dwellers were amphipods and clams *(Rangia cuneata)* which made up the bulk of the food, and smaller amounts of gastropods, mussels *(Congeria leucopheata)*, annelids, harpacticoid copepods, ostracods, isopods, and aquatic beetles.

Increase in size of the catfish was accompanied by a progressive increase in the utilization of large mobile animals which together made up almost one-half of the food of the largest size group. These larger animals included crabs *(Rithropanopeus harrisii* and *Callinectes sapidus)*, shrimp *(Macrobrachium ohione, Palaemonetes* sp., *Penaeus* spp., and *Callianassa* sp.) and fishes (*Anchoa mitchilli diaphana, Citharichthys spilopterus, Menidia beryllina, Micropogon undulatus,* and *Syngnathus* sp.), as well as unidentified remains referable to these categories.

Vegetation was virtually absent from the lower three size groups, although in the largest size of catfish it constituted 26 percent of the food material. Most of this vegetation was made up of dense mats of filamentous green algae (primarily *Cladophora* sp., although some *Rhizoclonium* sp. was noted). Since most of this vegetation appeared in the stomachs of seven specimens from only two collections made in February and March, it is probable that the percent of vegetation is somewhat exaggerated in this series of analyses. Detritus and unidentified organic material were most abundant in the smallest size group, making up 37 percent of the food volume in this group. This material declined thereafter to four percent in the largest fish.

Most of the smaller catfish appear to have concentrated upon one or a few food items, and only a relatively small number of foods figured prominently in this group as a whole. With increase in size an increase in diversity was noted, and in the upper size class a single fish (390 mm.) contained the following: 3 *Macrobrachium ohione*, 27 *Palaemonetes* sp., 5 palaemonids (undetermined), 13 *Callinectes sapidus*, 1 *Menidia beryllina* (70 mm.), 1 *Micropogon undulatus* (28 mm.), 2 *Syngnathus* sp. (90 mm. each), 1 fish (undetermined), and a trace of plant material.

As indicated in Figure 4, the degree of fullness of the stomachs suggests that some

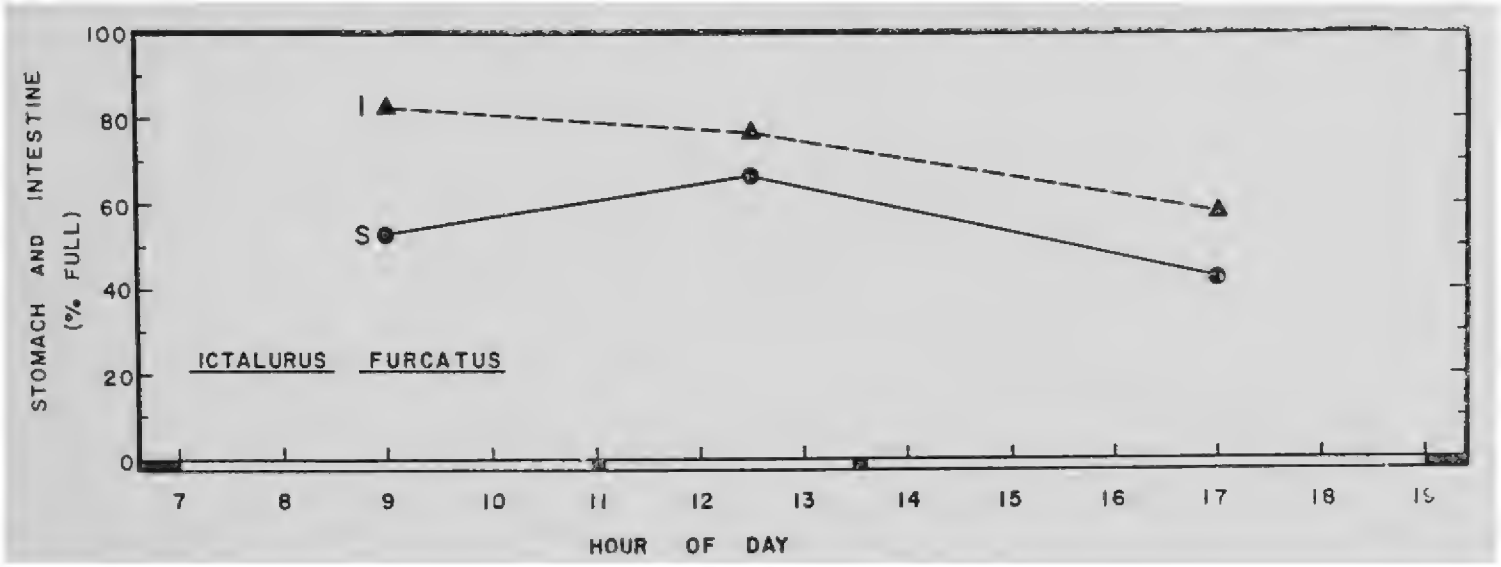

FIG. 4. Hourly pattern of percent-fullness of stomach and intestine of *Ictalurus furcatus*.

feeding must occur throughout the day with, perhaps, a diminution in feeding activity in the late afternoon and early evening. The condition of the intestines, however, points to the fact that the main feeding must take place either at night or in the early morning hours.

Although the food habits of the blue catfish are quite complex, three general feeding stages are recognizable. In smaller individuals a zooplankton-feeding stage is dependent chiefly upon calanoid copepods and schizopods. This stage appears to be largely completed by a size of 100 mm. A bottom-feeding stage dependent upon small bottom-inhabiting invertebrates is prominent in the 100–240 mm. catfish. Finally, a stage dependent primarily upon macro-mobile animals such as fishes, crabs, and shrimp achieves significance in catfishes over 200 mm. in length. This general pattern of food stages is displayed in common with a number of other species inhabiting Lake Pontchartrain, and it appears that from the standpoint of nutrition the blue cat is highly successful in the estuarine environment.

Ictalurus punctatus (Rafinesque). Channel Catfish

Food of the channel catfish in fresh water has been the subject of investigation by many workers. In a recent study, Bailey and Harrison (1948) reviewed a number of the more pertinent references including the following: Forbes (1888), Smith (1907), McAtee and Weed (1915), Shira (1917), Mobley (1931), Ewers and Boesel (1936), Aitken (1936), Boesel (1938), McCormick (1940), Dill (1944), Menzel (1945), and Dendy (1946). As indicated by these writers up to 98 percent of the diet of the very young channel catfish (less than 100 mm.) consists of small aquatic insects. With increase in size the catfish have been found to consume a much lower percentage of insects, and within wide ranges of tolerance, larger individuals appear to subsist upon whatever food happens to be locally available in quantity. Evidence indicates that many types of food materials are probably consumed in direct proportion to their availability.

Groups of channel catfish have been found to specialize at least temporarily upon algae, mollusks (especially gastropods), microcrustaceans, crayfish, insects (aquatic and terrestrial), and fishes. Even young of the same species have been found to enter the diet of the adults with a frequency proportional to their relative abundance in the fish population (Bailey and Harrison, 1948). In the Chickahominy River of Virginia Menzel (1945) found that algae and blue crabs formed a large proportion of the diet of this species when available. Because of this wide range of food tolerance, the channel catfish is generally considered to be omnivorous.

Fourteen specimens of channel catfish were examined from Lake Pontchartrain of which 13 contained food. Stomach contents of the 11 smaller individuals (76–119 mm.) consisted primarily of small bottom-living arthropods (isopods, amphipods, xanthid crabs, and chironomid larvae and pupae, as well as occasional microcrustaceans). Undetermined organic material and detritus made up about one-fourth of the stomach contents. Traces of foraminifera, filamentous algae, and vascular plants were present, and sand made up about eight percent of the material encountered. Two larger catfishes (207–312 mm.) had consumed quantities of crustaceans (isopods, xanthid crabs, and others), as well as smaller amounts of fish, hydroids, and undetermined organic matter.

In the brackish water environment of Lake Pontchartrain young channel catfish maintain themselves upon a diet composed primarily of small bottom crustaceans and insects together with bottom detritus. Food of the larger fish probably includes the same materials with the addition of fishes and large crustaceans as in the case of the related blue catfish. A wide variety of miscellaneous items appears to be consumed by both the young and adults.

Mugilidae

Mugil cephalus Linnaeus. Striped Mullet

Species of the genus *Mugil* are rather widely distributed throughout the tropical and subtropical shores of the world, and in some areas they assume a position of considerable importance in the economy of local human societies. Hence, it is not surprising that the food habits of the group in natural as well as artificial environments have received the attention of many workers. Much of this literature has recently been summarized by Pillay (1953), Thomson (1954), and Ebeling (1957). Most species of this genus are considered to feed upon plankton, filamentous algae, diatoms and other minute vegetable matter, or upon organic detritus and such nutritive material as may be procured by filtration of the bottom mud, although some divergence has been noted. Morphological and behavioral adaptations of these mugilids for obtaining and processing the nutriments are well known (see Ebeling, 1957, and the bibliography listed therein). The adults of most species browse upon the surface of shallow water sediments, and by means of a remarkable pharyngeal filtering device (supplemented by pharyngeal taste buds) they sort out the coarser materials which are expelled through the mouth. Finer filtered material receives mucus in the esophagus, and the mass is pulverized by the grinding action of the gizzard-like pyloric portion of the stomach. In the very long intestine the nutritive matter is digested from the mineral matter, apparently in the absence of either proteolytic or lipolytic enzymes (Ishida, 1935).

The food habits of *Mugil cephalus* have been discussed by several writers including Günther (1880), Linton (1904), Jordan (1905), Smith (1907), Jacot (1920), Hildebrand and Schroeder (1928), Ghazzawi (1933) (not seen), Hiatt (1947a-b), and Reid

(1955b). An excellent review of most of this literature was presented by Hiatt (1947a-b), therefore, only a summary will be undertaken here. It is generally agreed that the striped mullet feeds largely upon epiphytic algae, littoral diatoms, and finely divided organic detritus scraped from the surface layer of shallow mud flats or from the surface of roots and other objects present in such habitats. Remains of larger invertebrates and vascular plants sometimes appear among the ingested detritus, and the presence of planktonic crustacea and surface algae indicates that some plankton straining must also take place, especially among the younger individuals.

In the Lake Pontchartrain study 57 specimens of striped mullet (97–327 mm.) were examined, only 54 of which contained food. A few preliminary analyses of the contents of the muscular pyloric region of the stomachs yielded virtually no identifiable material, and it became necessary to include the contents of the cardiac region as well. Even examination of the material previous to grinding, however, provided little definitely identifiable matter, and since no clear distinctions could be made between the food of the different size groups, all specimens are treated below as a unit.

Almost one-half of the material encountered was classified as detritus and undetermined organic matter which seemed to have some cellular and tissue structure, although it was generally in an advanced state of decomposition. More than one-third of the substance appeared to be mud. silt, and sand, and only about 14 percent could be definitely recognized. Eleven percent of the material was of vascular plant origin, but could not be categorized further. About two percent was algal in nature including both flat and filamentous algae and littoral diatoms (*Biddulphia* sp., *Terpsinoë* sp., and others). Miscellaneous fish scales, foraminifera, sponge spicules, and minute gastropods each constituted less than one percent of the contents.

These results indicate that in Lake Pontchartrain, as elsewhere, the striped mullets are iliophagous and that their food consists chiefly of bottom surface material. Decomposing organic matter, detritus, and mud were much too abundant to be considered incidental in the food of the species, and it was not possible to detect any significant indictations of selectivity for the minor items such as algae, foraminifera, minute gastropods, etc. Undoubtedly some selection in feeding site does take place based primarily upon taste and size and consistency of the particles. This study suggests that the vegetable matter itself, or the decomposing bacteria, or a combination of the two factors may have influenced the feeding site of the mullets examined. Field observations indicated that striped mullet do feed at the surface, and schools were occasionally observed to be actively feeding upon surface scums of *Anabaena* spp. which were seasonally abundant. This material was not encountered, however, during the course of stomach analyses. Judging from the degree of fullness of the alimentary tracts, striped mullets appear to feed throughout the day, and on the basis of what is known of other iliophagous species (Gneri and Angelescu, 1951), it is probable that they feed throughout most of the night as well.

Atherinidae

Menidia beryllina (Cope). Silverside

Hildebrand and Schroeder (1928) examined the stomachs of 20 silversides from Chesapeake Bay and encountered the following food items (listed in order of importance): small crustaceans, small mollusks, insects, worms, and a few strands of algae. Reid (1954) found that in the Cedar Key area of Florida the food of this species con-

sisted primarily of plankton organisms, especially copepods, as well as some algae and amphipods. Six specimens taken under night lights contained freshly-ingested insects.

In the smallest size class of silversides examined from Lake Pontchartrain, calanoid copepods made up six percent of the food, although they were practically absent from individuals above 55 mm. (Table 4 and Fig. 5). These copepods undoubtedly represent

TABLE 4

Occurrence of food items in digestive tracts of 60 *Menidia beryllina*

	40.0–54.0 mm.		55.0–64.0 mm.		65.0–79.0 mm.	
	21 examined 19 with food		20 examined 20 with food		19 examined 16 with food	
FOOD ITEMS	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume
Ostracoda	.....	.....	5.0	T	5.3	.....
Copepoda						
Calanoid	9.5	5.5	5.0	0.4	.....	.....
Mysid shrimp	4.5	3.0	15.0	10.5	10.5	2.5
Isopoda	38.1	42.3	30.0	12.4	10.5	0.3
Amphipoda	42.9	18.9	70.0	58.7	73.7	61.0
Insecta (undet.)	9.5	0.5	20.0	2.8	21.1	0.5
Coleoptera	.....	.....	.....	.....	5.3	.....
Diptera—larvae	4.8	1.5	10.0	0.4	.....	.....
Pupae, adults	9.5	3.0	15.0	4.4	21.1	15.4
Hymenoptera	14.3	5.3	10.0	4.5	5.3	9.9
Arachnida	.....	.....	.....	.....	5.3	0.1
Annelida	4.8	.....	.....	.....	.....	.....
Hydroids	4.8	.....	.....	.....	.....	.....
Vertebrata						
Fish remains	9.5	.....	5.0	T	10.5	.....
Algae—filamentous	4.8	.....	15.0	0.1	10.5	0.2
Vascular plants	4.8	0.6	5.0	.....	.....	.....
Eggs and cysts	.....	.....	5.0	.....	.....	.....
Organic mat. (undet.)	47.6	17.0	70.0	5.0	73.7	9.5
Detritus	33.3	2.5	35.0	0.3	15.8	0.5
Sand	9.5	.....	5.0	0.7	.....	.....
SUMMARY						
Copepoda		5.5		0.4		0.0
Mysid shrimp		3.0		10.5		2.5
Isopoda		42.3		12.4		0.3
Amphipoda		18.9		58.7		61.0
Insect pupae, adults		8.8		11.7		25.8
Misc. Invertebrates		2.1		0.5		0.3
Incidental, Undet.		19.5		6.0		10.0

* Stomach and intestine included.

the remnants of an earlier important zooplankton-feeding stage in individuals less than 40 mm.

Isopods and amphipods together made up the bulk of the food, constituting from 61 percent to 71 percent of the stomach contents in all size classes. Stomach analysis records indicate isopods were abundant in the 40–54 mm. size class and declined thereafter to less than one percent in the largest fish. Although *Leptochelia* sp. and a number of other tanaids and anthurids were definitely recognized, it appears now that at least some of these crustaceans identified as isopods may in reality have been dorso-ventrally flattened amphipods. Whatever the taxonomic position of these forms may be, they should eventually provide important evidence regarding the feeding site of the young silversides. Other species of amphipods displayed a progressive increase from 19 percent

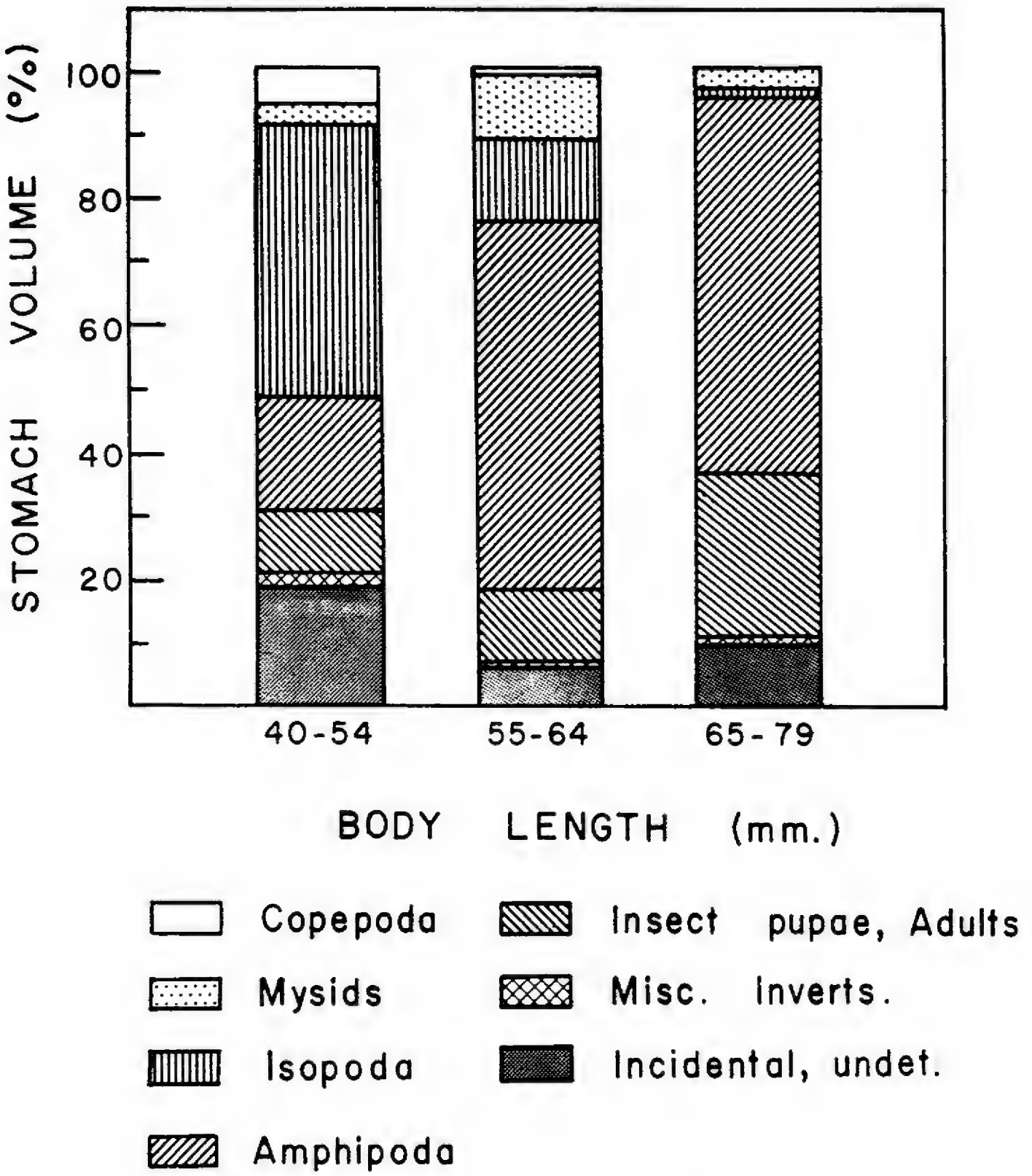

FIG. 5. Ontogenetic food progression of *Menidia beryllina*.

to 61 percent. These included primarily *Corophium* spp. in addition to a number of gammarids and a few tube dwellers (probably *Cerapus sp.*). A progressive increase in the consumption of insects from 9 percent to 25 percent involved primarily an increase in the utilization of chironomid pupae and adults, although some ants and a single beetle also were taken.

Schizopods were present in all size groups. but they were most abundant in the intermediate fish where they made up 11 percent of the food. Detritus and undetermined organic matter constituted 20 percent of the food of the smallest silversides and declined in the larger size groups. Miscellaneous items included filamentous algae and vascular plant material as well as annelids, ostracods. chironomid larvae. arachnids. eggs and cysts. and fish remains.

Although not demonstrated by the present series, the very young silversides probably pass through a zooplankton-feeding stage dependent primarily upon calanoid copepods.

at which time they are either pelagic or benthic inhabitants of the open water (see Hubbs', 1921, discussion of the behavior and habitat of the fresh-water atherinid, *Labidesthes sicculus*). With increasing size this voracious and adaptable little fish moves into shallow waters where it forages among the emergent hydrophytes collecting small arthropods such as ants, beetles, and spiders which fall into the water. It is also active among the submerged vegetation where it obtains quantities of isopods, amphipods, and other small invertebrates. Direct observations and the presence in the stomachs of tube-dwelling amphipods and chironomid larvae indicate that some foraging may take place at the surface and bottom in deeper water. Gunter (1945) has noted a movement by larger individuals to more saline waters.

As indicated by Figure 6, young silversides appear to feed both in the morning and in the afternoon, whereas the adults feed primarily in morning. Although the feeding habits are undoubtedly correlated with the availability of the food items, detailed conclusions can not be drawn because of inadequate knowledge of the habits and habitats of the invertebrates. Young silversides consumed the creatures identified as isopods largely in the afternoon, whereas the adults ate amphipods chiefly in the morning. As mentioned earlier, Reid (1954) found evidence of feeding under night lights.

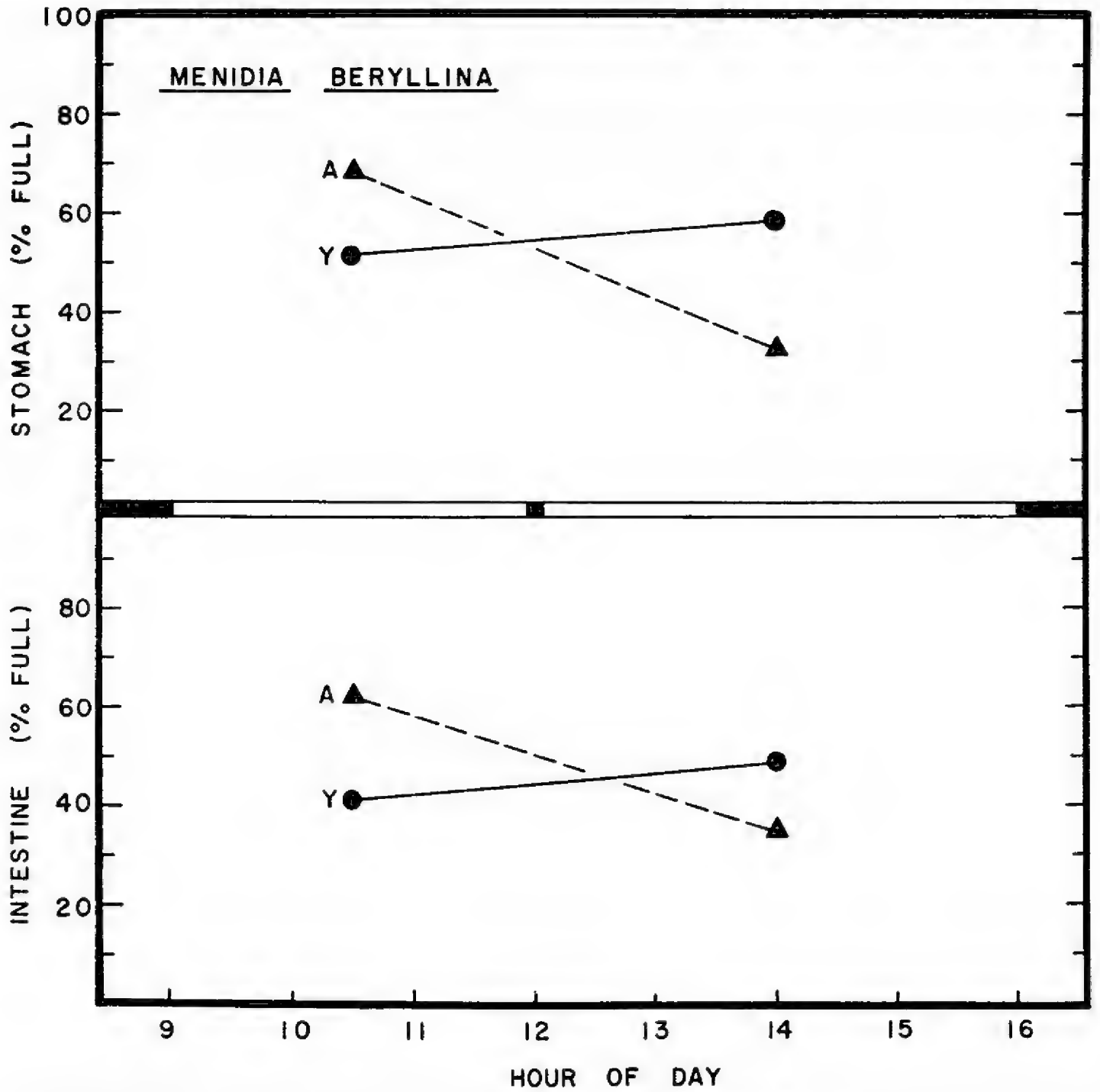

FIG. 6. Hourly pattern of percent-fullness of stomach and intestine of *Menidia beryllina* (young and adult).

SERRANIDAE

Morone interrupta Gill. Yellow Bass

Studies on the food of the yellow bass from fresh water by Forbes (1878, 1880a, b), Hildebrand and Towers (1927), and McCormick (1940) indicate that the species consumes small aquatic animals including entomostraca, aquatic insect larvae, and small fishes, as well as occasional bits of vegetation and some terrestrial insects. The food of the species in brackish-water environments apparently has been studied only by Lambou (1952) who examined the stomach contents of 273 large specimens (*ca.* 127–292 mm.) taken from the marshes bordering the northeastern shore of Lake Pontchartrain. Only 167 of these fish contained food. Fish, insects, vegetable matter, and unrecognizable organic material were each encountered in less than five percent of the stomachs. Crabs and penaeid shrimp, each appeared in about 30 percent of the stomachs, and palaemonid shrimp in about 10 percent, indicating a high percentage of crustaceans consumed in the brackish-water marshes.

In the present study crustaceans made up over half of the food material and included 24 percent shrimp (schizopods, juvenal penaeids, *Palaemonetes* sp., and *Macrobrachium ohione*) and 28 percent crabs (*Callinectes sapidus* and *Rithropanopeus harrisii*) (Table 5). Fishes constituted 35 percent of the stomach contents and included *Cynos-*

TABLE 5

Occurrence of food items in digestive tracts of 27 *Morone interrupta*

	130.0–195.0 mm.	
	27 examined 18 with food	
FOOD ITEMS	Percentage of tracts* containing item	Percentage of total stomach volume
Copepoda (Arguloid)	3.7	0.1
Mysid shrimp	18.5	18.2
Isopoda	7.4	0.3
Amphipoda	22.2	2.1
Palaemonid shrimp (undet.)	7.4	0.1
Palaemonetes sp.	3.7	4.8
Macrobrachium ohione	3.7	1.1
Crabs		
Rithropanopeus harrisii	22.2	18.0
Callinectes sapidus	18.5	9.7
Insecta (undet.)	3.7	.....
Diptera	7.4	.....
Odonata	3.7	0.1
Annelida	3.7	0.3
Hydroids	3.7	T
Sponge	7.4	.....
Vertebrata		
Cynoscion sp.	3.7	7.7
Cyprinodon variegatus	3.7	0.5
Gobiosoma bosci	3.7	4.8
Micropogon undulatus	3.7	1.1
Mollienesia latipinna	3.7	4.3
Fish remains	29.6	16.5
Algae—filamentous	3.7	0.1
Organic mat. (undet.)	63.0	6.8
Detritus	18.5	3.5
SUMMARY		
Microcrustacea		20.7
Macrocrustacea		33.7
Fishes		34.9
Miscellaneous, Undet.		10.8

* Stomach and intestine included.

cion sp., *Cyprinodon variegatus, Gobiosoma bosci, Micropogon undulatus, Mollienesia latipinna,* and other small forms. Undetermined organic material and detritus constituted 11 percent of the food volume, and incidental items included filamentous algae, sponge, hydroid, annelids, arguloid copepods, isopods, amphipods, and odonate and dipteran insects.

The above studies point to the fact that the yellow bass is a predatory species which in the brackish-water environment takes in a variety of shrimps, crabs, and fishes. The presence of bits of filamentous algae, sponge, and hydroid in the Lake Pontchartrain specimens indicates feeding near the bottom, either around the shallow margins of the lake or near the mouths of freshwater passes.

Centrarchidae

Micropterus s. salmoides (Lacépède). Northern Largemouth Bass

The food of the largemouth bass in freshwater environments has been extensively investigated, and since the literature has recently been reviewed in some detail by McLane (1948) it need not be reiterated here. In general, these works have shown that with increasing size there occurs a progressive change in the food of this species from microcrustaceans to insects to fishes, although crayfish and other arthropods may also form important portions of the adult diet.

McLane, himself (*op. cit.*), carried out a study of the seasonal food habits of the largemouth bass in St. Johns River of Florida where a number of estuarine species were available for consumption. He found that very young bass consumed large amounts of cladocera and other entomostraca. In slightly larger fish these items were replaced by schizopods. Bass belonging to larger size groups fed chiefly upon macrocrustacea (*Palaemonetes paludosa, Procambarus fallax,* and *Rithropanopeus harrisii*) and at least twenty-five species of fishes, many of which are also available in Lake Pontchartrain.

Lambou (1952) examined the stomachs of 93 largemouth bass (*ca.* 203–432 mm.) taken from the marshes bordering the northeastern shore of Lake Pontchartrain. Fifty-three of these bass contained food. Crabs were present in 56 percent of the stomachs, "shrimp" (presumably *Penaeus* spp.) appeared in 25 percent, "freshwater shrimp" (presumably *Macrobrachium ohione* and *Palaemonetes* sp.) and insects appeared in 7 percent each. and vegetable matter and undetermined material in 2 percent each. Thus, crabs and shrimp made up the bulk of the diet of the largemouth bass in the marshes, whereas fish and other materials were of much less importance.

Three specimens of the largemouth bass (175–209 mm.) from Lake Pontchartrain were examined in the present study, only two of which contained food. This material included a single grass shrimp (*Palaemonetes* sp.) and five small blue crabs (*Callinectes sapidus*) which together made up 97 percent of the stomach contents. Additional material included vegetation (*Vallisneria spiralis* and the filamentous green alga, *Cladophora* sp.), as well as small amounts of undetermined organic material and detritus. These studies together with those of McLane (*op. cit.*) and Lambou (*op. cit.*) demonstrate that when available a number of species of estuarine invertebrates and fishes are readily utilized by the largemouth bass.

Carangidae

Caranx hippos (Linnaeus). Common Jackfish

Food habits of the common jackfish have been reported by Linton (1904), Hildebrand and Schroeder (1928), Knapp (1949), and Reid (1954). These authors have found this fish to be highly predatory consuming large quantities of fishes and crabs, as well as smaller percentages of squids, shrimp, and smaller invertebrates.

Only a single young specimen of the common jack (79 mm.) from Lake Pontchartrain was examined, and this contained one anchovy (*Anchoa mitchilli diaphana*) 30 mm. in length which constituted about 98 percent of the stomach contents. A small amount of undetermined matter also was present. Although only a few jacks were captured and only a single specimen was examined for food, many jacks were observed in the open waters of Lake Pontchartrain. These were generally presumed to be actively feeding at the surface upon small fishes, probably clupeids and engraulids.

Sciaenidae

Aplodinotus grunniens Rafinesque. Freshwater Drum

Studies on the food of the freshwater drum by Forbes (1878, 1880a, b), Forbes and Richardson (1920), Hildebrand and Towers (1927), Rimsky-Korsakoff (1930), Ewers (1934), and Dendy (1946) have indicated that in fresh waters this species normally passes through a series of ontogenetic food stages. Thus, the smallest individuals feed upon entomostracans. These are followed by aquatic insects, and the large drums feed chiefly upon clams and snails, supplemented by crayfish and other material. Dendy (1946) has pointed out that if insects and mollusks are essentially unavailable the drum may get along by abbreviating the insect-feeding stage and by replacing the mollusk-feeding stage with one dependent upon small fishes.

In the present study five specimens of the freshwater drum (211–347 mm.) from Lake Pontchartrain were examined, of which only four contained food. This material included 73 percent clams (*Congeria leucopheata* and *Rangia cuneata*), 11 percent mud crabs (*Rithropanopeus harrisii*), 10 percent undetermined organic material, and 6 percent amphipods. Additional items present in trace amounts included remains of blue crabs (*Callinectes sapidus*), gastropods, hydroids, and leaves and twigs of vascular plants. The food of this species appears to be quite similar to that of the young black drum.

Bairdiella chrysura (Lacépède). Silver Perch

Food habits of the silver perch have been studied by Linton (1904), Welsh and Breder (1923), Hildebrand and Schroeder (1928), Hildebrand and Cable (1930), Reid (1954), and Reid, Inglis, and Hoese (1956). These workers have shown that the chief food of the smallest silver perch is copepods supplemented by smaller amounts of ostracods, cladocera, schizopods, amphipods, and chaetopods. With increase in size there is greater emphasis upon annelids and larger crustaceans (schizopods, amphipods, isopods, small shrimp, and crabs) with occasional mollusks. Largest individuals have been reported to consume a few anchovies and other fishes, as well. These considerations led Hildebrand and Cable (*op. cit.*) to conclude that the silver perch feeds largely on the bottom and is strictly carnivorous.

The food of the silver perch from Lake Pontchartrain was made up of four primary types, each constituting roughly a quarter of the total stomach volume. These included schizopods, larger shrimp, fishes, and miscellaneous material (including smaller invertebrates and detritus) (Table 6). Stomachs of the silver perch frequently were packed

TABLE 6

Occurrence of food items in digestive tracts of 41 *Bairdiella chrysura*

	70.0–143.0 mm.	
	41 examined 20 with food	
FOOD ITEMS	Percentage of tracts* containing item	Percentage of total stomach volume
Copepoda	4.8	.....
Mysid shrimp	14.6	24.3
Isopoda	7.3	8.3
Amphipoda	2.4	0.8
Palaemonid shrimp	7.3	19.8
Penaeid shrimp	12.2	6.1
Crabs		
Rithropanopeus harrisii	7.3	1.0
Callinectes sapidus	2.4	2.4
Vertebrata		
Anchoa mitchilli	7.3	12.1
Fish remains	12.2	12.3
Vascular plants	2.4	0.2
Organic mat. (undet.)	53.7	12.5
Sand	9.8	.....
SUMMARY		
Mysid shrimp	24.3	
Palaemonid, Penaeid shrimp	25.9	
Isopoda, Amphipoda	9.1	
Crabs	3.4	
Fishes	24.4	
Incidental, Undet.	12.7	

* Stomach and intestine included.

with schizopods, and one individual contained more than 100 of these small crustaceans. Larger shrimp included grass shrimp (chiefly *Palaemonetes pugio*) and considerable numbers of young penaeids. Fish food included mainly *Anchoa mitchilli diaphana* as well as unidentified remains, and one large silver perch had swallowed a 40 mm. anchovy. The miscellaneous material encountered in the stomachs included copepods, isopods (*Aegathoa* sp.), and crabs (*Callinectes sapidus* and *Rithropanopeus harrisii*), as well as a small amount of vascular plant material and sand. Undetermined organic material made up 13 percent of the contents.

On the basis of present knowledge of the food of the silver perch, two general feeding stages may be recognized, an early copepod-feeding stage which is completed before a length of 50 mm. and a later schizopod-palaemonid-penaeid shrimp stage. In this second stage a great variety of other invertebrates as well as occasional fishes are consumed. Further work will undoubtedly result in the recognition of subdivisions of the shrimp-feeding stage of this voracious fish. In Lake Pontchartrain the food of the silver perch overlaps that of many other species and appears especially similar to that of young speckled trout (*Cynoscion nebulosus*) of comparable size.

Cynoscion arenarius Ginsburg. Sand Trout, Sand Squeteague

The food of the sand trout in Florida and Texas has been investigated by Reid (1954, 1955b, 1956) and by Reid, Inglis, and Hoese (1956). These workers have indicated that trout less than 60 mm. subsist largely upon small crustaceans (copepods, larval and metamorphosing shrimp and crabs, and others). Shrimp, although consumed to some extent by trout of all sizes, appeared to be an important element in the diet of the intermediate-sized trout. Fishes were found to be consumed by sand trout as small as 34 mm., and they were present in the stomachs of at least four-fifths of all trout over 80 mm. in length. Among the fishes consumed, the menhaden (*Brevoortia patronus*) was the most conspicuous, although other clupeids, anchovies, and young sciaenids were also noted. The presence of young sand trout indicated cannibalism. Miscellaneous items included crustacean and molluscan debris, as well as undetermined organic matter.

In the smallest sand trout (40–99 mm.) from Lake Pontchartrain schizopods constituted almost one-third of the food volume, and traces of other small invertebrates included amphipods, palaemonid shrimp, and bits of crabs (Table 7 and Fig. 7). These small invertebrates were almost entirely absent from the food of the larger size groups.

Fish remains constituted over one-half of the food of the smallest sand trout examined, and this material increased to over 90 percent of the stomach contents in the larger trout (150–225 mm.). Fishes consumed included *Anchoa mitchilli diaphana* and the remains of other unidentified species, probably young clupeids. Penaeid shrimp made up 8 per-

TABLE 7

Occurrence of food items in digestive tracts of 64 *Cynoscion arenarius*

FOOD ITEMS	40.0–99.0 mm. 22 examined 18 with food		100.0–149.0 mm. 29 examined 21 with food		150.0–225.0 mm. 13 examined 8 with food	
	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume
Mysid shrimp	45.5	31.9	3.4	1.0	.....	.....
Amphipoda	9.1	0.2	.....	.....	.....	.....
Palaemonetes sp.	4.5	2.7	.....	.....	.....	.....
Penaeus sp.	.....	.....	.....	.....	7.7	7.7
Crabs (undet.)	4.5	2.7	.....	.....	.....	.....
Annelida	.....	.....	3.4	T	.....	.....
Mollusca						
Rangia cuneata	4.5	.....	.....	.....	.....	.....
Gastropoda	.....	.....	3.4	0.4	.....	.....
Hydroids	.....	.....	3.4	.....	.....	.....
Vertebrata						
Anchoa mitchilli	4.5	10.2	37.9	54.1	30.8	56.7
Fish remains	45.5	44.1	37.9	28.9	53.8	34.1
Algae—filamentous	.....	.....	3.4	0.1	.....	.....
Organic mat. (undet.)	68.2	7.7	72.4	15.3	23.1	1.5
Detritus	40.9	0.4	6.9	.....	15.4	.....
Sand	.....	.....	3.4	0.1	.....	.....
SUMMARY						
Microcrustacea		32.1		1.0		0.0
Macrocrustacea		5.4		0.0		7.7
Fishes		54.3		83.0		90.8
Misc. and Undet.		8.1		15.9		1.5

* Stomach and intestine included.

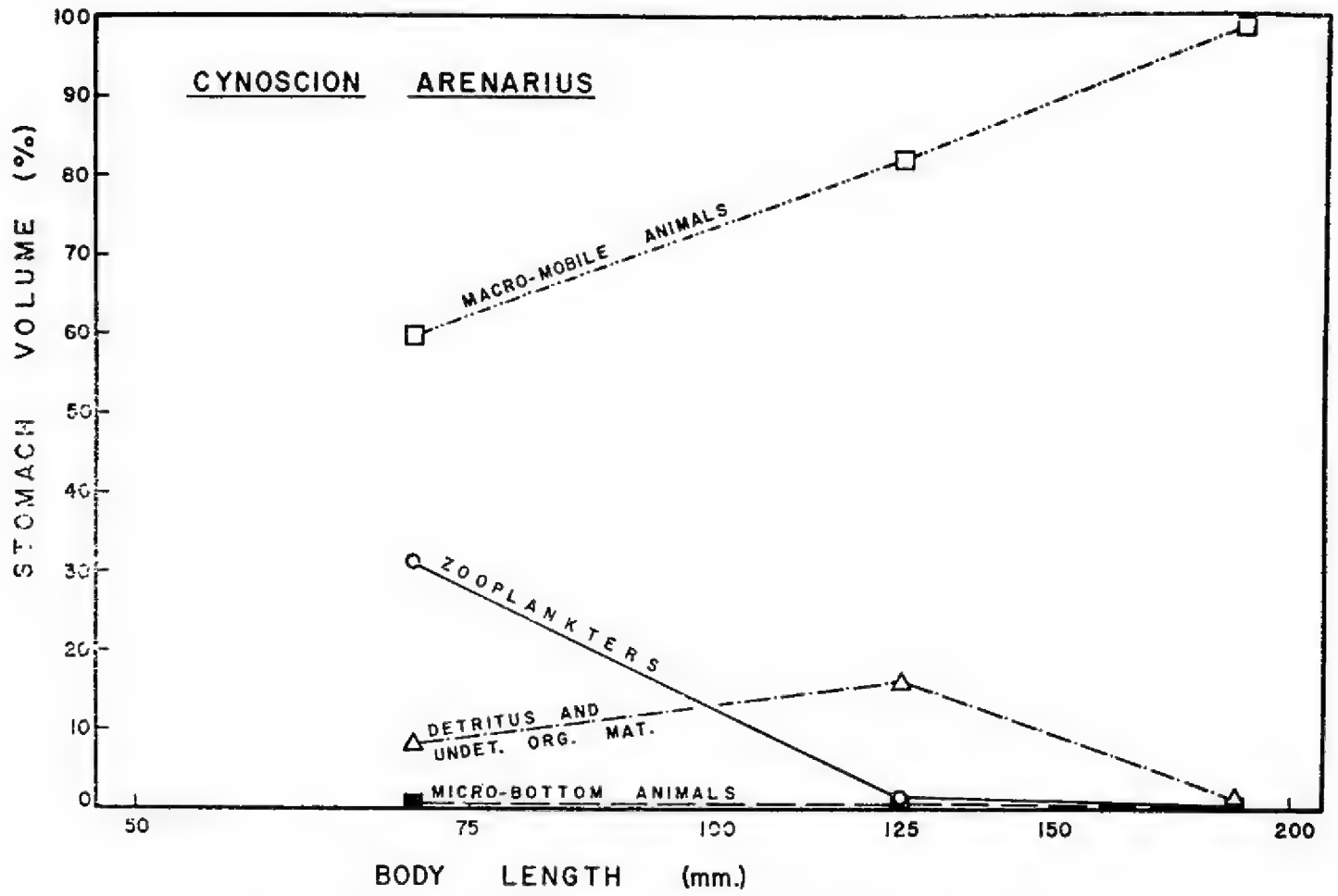

FIG. 7. Ontogenetic food progression of *Cynoscion arenarius*.

cent of the food of the adults. Undetermined organic material and detritus constituted 8–15 percent of the food of sand trout less than 150 mm., although such material was scarcely represented in the food of the larger fish. Incidental items included traces of mollusk shells, annelids, hydroids, filamentous algae, and sand.

On the basis of the work of Reid (*op. cit.*) it appears that the youngest sand trout pass through a copepod-feeding stage. This is followed in Lake Pontchartrain by a schizopod-feeding stage which grades into the piscivorous adult, dependent chiefly upon the anchovy. This predatory fish is highly selective in its food habits and consumes surprisingly few incidental items. The virtual absence of sand and vascular plant remains from the stomach contents points to the fact that sandy bottoms and vegetation beds are probably not primary feeding sites.

Cynoscion nebulosus (Cuvier and Valenciennes).

Speckled Trout, Spotted Squeteague

The food habits of the speckled trout have received the attention of a number of workers. Linton (1904) found that 18 specimens had consumed chiefly fish and shrimp. Hildebrand and Schroeder (1928) concluded from examination of the stomachs of 20 individuals that small trout feed mainly upon crustaceans, whereas large trout consume primarily fish. Pearson (1929) examined the stomachs of 220 specimens (60–600 mm.) from Texas. His data indicate that shrimp and fishes were the predominant foods, and throughout the size range investigated shrimp appeared about twice as frequently as fishes. Species of fishes encountered included the young of *Leiostomus xanthurus*, *Micropogon undulatus*, and *Mugil* sp., as well as both young and adult of *Anchoa* sp. and *Menidia* sp. He also noted that "grass-dwelling" gobies were extensively consumed, and crabs were found in a few of the larger specimens.

Gunter (1945) reported on the analyses of 153 stomachs of adult speckled trout (275–555 mm.) from southern Texas, 93 of which contained food. Crustaceans including palaemonid shrimp (*Palaemonetes* sp.), penaeid shrimp (*P. setiferus* and either *P. aztecus* or *P. duorarum*), and the blue crab (*Callinectes sapidus*) were present in 3 to 20 stomachs each. Fishes, however, constituted the most important food material and included *Mugil cephalus* in 18 stomachs, and *Menidia peninsulae, Cyprinodon v. variegatus, Brevoortia* sp., *Lagodon rhomboides, Orthopristes chrysopterus,* and *Lucania parva venusta,* each occurring in 5 stomachs or less. Speckled trout were noted to consume fishes more than one-half their own body length. Knapp (1949) analyzed the stomach contents of 2,698 speckled trout from Texas. Of this number 70 percent had fed on shrimp, and over 33 percent on fishes, whereas squids, crabs, and other invertebrates were each present in less than 10 percent of the stomachs.

Moody (1950) conducted a detailed study of the food of the speckled trout at Cedar Key, Florida. Of the 954 stomachs analyzed only 511 contained food. Moody found that during its life history the speckled trout passes through four recognizable feeding stages, in which it specializes alternately upon copepods, caridean shrimp, penaeid shrimp, and fishes. Copepods, which were prominent in the diet of small trout up to about 30 mm., had almost completely disappeared by the 50 mm. stage. Schizopods formed an important supplement in the 20–70 mm. group. Caridean shrimp reached a peak in the 50–80 mm. group, constituting up to 80 percent of the stomach contents of this size group. The percentage of caridean shrimp declined gradually, and they were less frequent in the food of the adults. These shrimp included, in the order of abundance, *Hippolyte* sp., *Angasia carolinense, Periclimenes longicaudatus, Palaemonetes pugio* and *Palaemonetes intermedius, Periclimenes americanus,* and *Palaemon floridanus,* as well as an unidentified crangonid. Moody pointed out that a shift in food habits takes place around 150 mm., and that above this size the speckled trout assumes the diet of the adult, i.e. penaeid shrimp and fishes. Penaeid shrimp (*P. duorarum*) were most prominent in the food of the 150–300 mm. class, being replaced thereafter by fishes. Both young and adult trout were noted to consume quantities of fishes, and whereas *Anchoa mitchilli* was the principal fish food in size classes below 150 mm., *Lagodon rhomboides* was most important in the diet of larger individuals. Additional fish species encountered included *Cynoscion nebulosus* in the stomachs of 3 adults (indicating cannibalism), *Mollienesia latipinna* encountered twice, and *Mugil cephalus, Menidia* sp., *Gobiosoma* sp., *Bairdiella chrysura, Chloroscombrus chrysurus,* and a scombrid only once. Miscellaneous food items included sponge, shell, amphipods, stomatopods, portunid crabs, tunicates, and a wood fragment. Grass particles were present in 10 percent of the stomachs. On the basis of the above information Moody concluded that the speckled trout is a voracious feeder preferring live active food, a conclusion also reached by Eigenmann (1902) regarding the related species *C. regalis.*

In the smallest speckled trout (40–99 mm.) from Lake Pontchartrain small crustaceans made up 44 percent of the food material (Table 8 and Fig. 8). These included the more planktonic schizopods (20 percent), bottom-living isopods and amphipods (18 percent), and a lower percentage of palaemonid shrimp (6 percent). Small fishes made up almost one-half of the food of the young trout and included *Anchoa mitchilli diaphana,* undetermined larvae, and other fish remains. Undetermined organic material comprised eight percent of the stomach contents.

In all size groups above 100 mm. shrimp and fishes predominated, constituting over

TABLE 8

Occurrence of food items in digestive tracts of 66 *Cynoscion nebulosus*

FOOD ITEMS	40.0–99.0 mm. 10 examined 9 with food		100.0–149.0 mm. 17 examined 14 with food		150.0–199.0 mm. 10 examined 8 with food		200.0–406.0 mm. 29 examined 17 with food	
	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume
Copepoda (Arguloid)	10.0	T	.....	.....	.....	.....	.....	.....
Mysid shrimp	50.0	19.9	.....	.....	.....	.....	.....	.....
Isopoda	40.0	2.1	5.9	0.2	.....	.....	.....	.....
Amphipoda	50.0	16.2	.....	.....	10.0	.....	.....	.....
Palaemonetes sp.	10.0	6.1	.....	.....	10.0	17.2	3.4	0.1
Penaeus sp.	.....	.....	11.8	14.2	.....	.....	6.9	4.9
Crabs	.....	.....	5.9	2.8	.....	.....	3.4	0.4
Insecta	.....	.....	.....	.....	10.0	.....	.....	.....
Hydroids	.....	.....	5.9	.....	.....	.....	.....	.....
Vertebrata								
Anchoa mitchilli	10.0	12.1	11.8	28.4	30.0	62.1	10.3	40.9
Micropogon undulatus	.....	.....	5.9	14.2	10.0	9.3	3.4	6.5
Fish larvae	10.0	12.1	.....	.....	.....	.....	.....	.....
Fish remains	40.0	24.1	35.3	32.1	20.0	1.4	51.7	40.8
Algae—filamentous	.....	.....	.....	.....	.....	.....	3.4	0.8
Vascular plants	.....	.....	11.9	1.5	10.0	1.7	3.4	2.7
Seeds	.....	.....	5.9	.....	.....	.....	.....	.....
Organic mat. (undet.)	60.0	8.0	58.8	6.6	60.0	6.6	24.1	2.0
Detritus	30.0	.....	11.9	T	50.0	1.7	20.7	0.8
Sand	.....	.....	11.9	0.3	10.0	.....	6.9	0.3
SUMMARY								
Microcrustacea		38.2		0.2		0.0		0.0
Macrocrustacea		6.1		17.0		17.2		5.4
Fishes		48.3		74.7		72.8		88.2
Misc. and Undet.		8.0		8.4		10.0		6.6

* Stomach and intestine included.

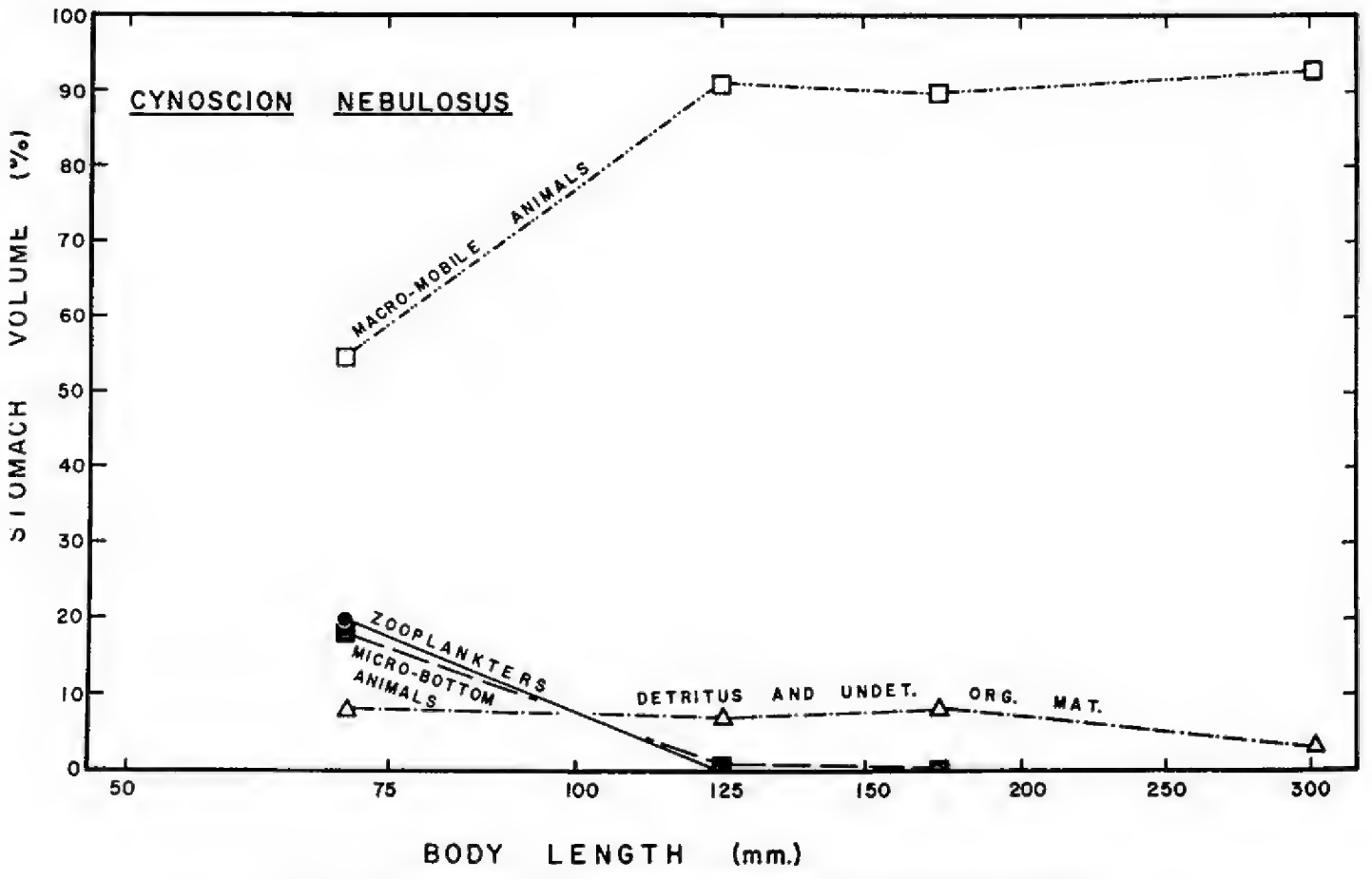

FIG. 8. Ontogenetic food progression of *Cynoscion nebulosus*.

90 percent of the food volume in the adults. Both palaemonid and penaeid shrimp were taken, and these shrimp together, made up one-sixth of the food of the 100–200 mm. individuals. The fish food of the adult trout included *Anchoa mitchilli diaphana* (30–60 percent), small *Micropogon undulatus* (7–14 percent), and large quantities of unidentified fish remains (definitely clupeiform and probably *Brevoortia patronus*). Small amounts of vascular plant remains were uniformly present in the stomachs of the adults. Detritus and undetermined organic material made up only a small percentage of the stomach contents, and miscellaneous items included algae and seeds, as well as hydroids, crabs, and insects.

Although very small speckled trout (less than 40 mm.) were not included in the present study, the investigations of Moody (*op. cit.*) demonstrated that very young individuals subsist almost entirely upon copepods. In the Lake Pontchartrain specimens a schizopod-amphipod feeding stage was indicated in the 40–100 mm. size class and, perhaps, traces of a palaemonid-penaeid shrimp stage in the 100-200 mm. group. The predominant food of the subadult and adult speckled trout, however, was fishes. These entered the diet early, and they comprised one-half of the food the smaller trout (40–99 mm.) and three-quarters of the food of the adults.

Judging from the degree of fullness of the stomachs (Fig. 9), the speckled trout feeds heavily in the early to mid-morning hours and takes in little, if anything, during the afternoon. In this respect it apparently differs from the sand trout which feeds earlier in the morning and which appears to resume feeding in the mid-afternoon.

A number of authors including Pearson (1929), Moody (1950), Pew (1954), and Reid (1956) have discussed the habitat relations of the speckled trout in Florida and

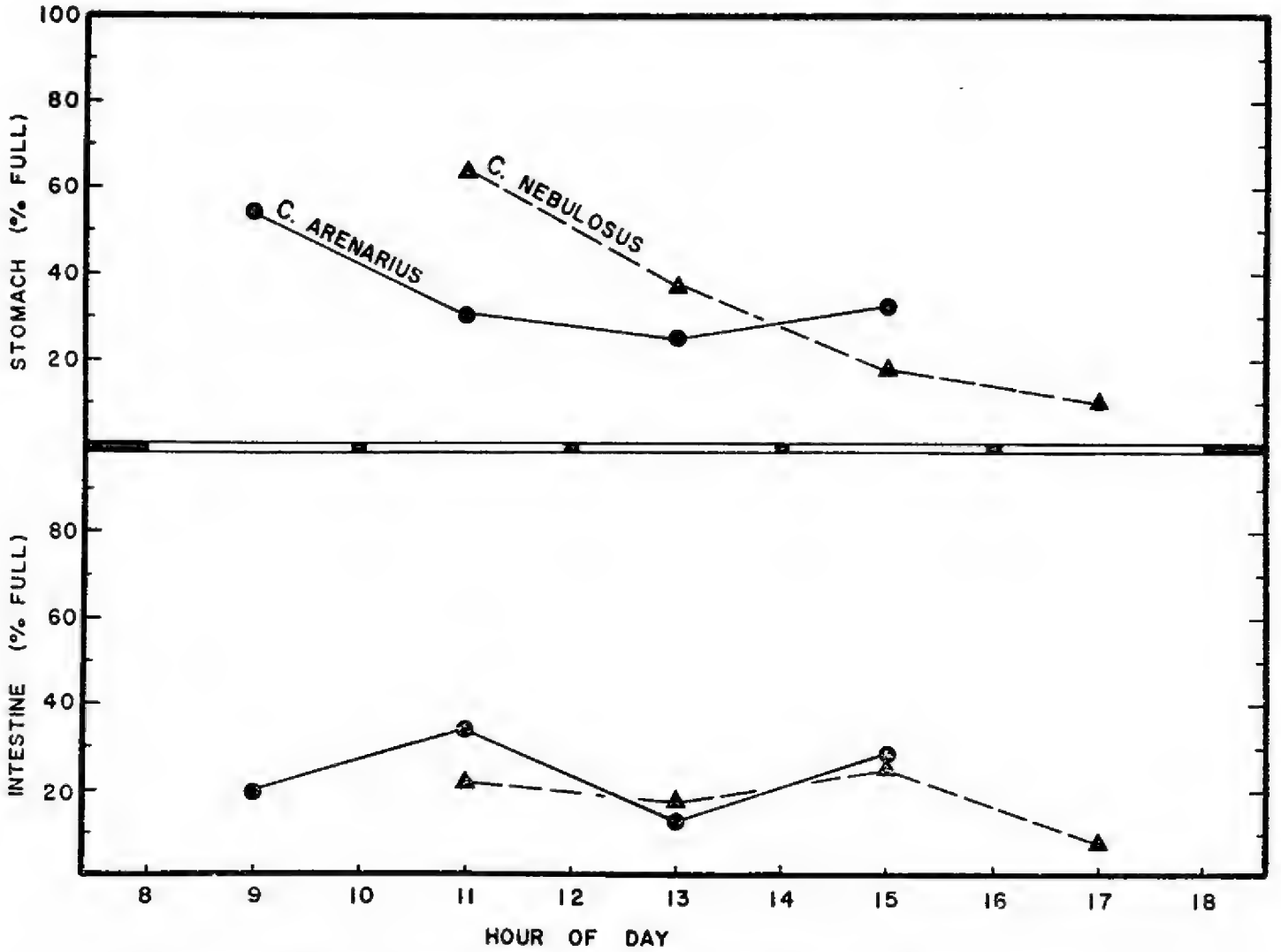

FIG. 9. Comparison of hourly patterns of percent-fullness of stomach and intestine of *Cynoscion arenarius* and *C. nebulosus*.

Texas, and they have generally agreed that the speckled trout is an inhabitant of clear waters with heavy grass bottom. These authors have pointed out that young trout seem to be critically associated with quiet shallow lagoons and coves possessing grassy flats where they consume great numbers of caridean shrimp. Adults, on the other hand, have been noted to remain in deeper water although frequently coming into the shallow grassy areas to feed upon shrimp and small fishes, especially the pinfish.

On *a priori* grounds, therefore, it might be assumed that the speckled trout would not regularly inhabit Lake Pontchartrain which is characterized by high turbidity and sparse grassy flats. In view of their presence in the lake, some deviation from the accepted patterns of food and habitat utilization by resident individuals is not at all surprising. In the virtual absence of weed beds caridean shrimp were essentially unavailable and were insignificant in the diet of the young trout. Likewise, as mentioned above, very few penaeid shrimp were taken. This may have been due in part to the relative absence from Lake Pontchartrain of the pink shrimp *(P. duorarum)* (see Darnell and Williams, 1956), which is the staple penaeid for the Florida population, or to greater difficulty in locating and apprehending the mud-loving brown and white shrimp (*P. aztecus* and *P. setiferus*) which are abundant in the lake. Finally, in the virtual absence of weed beds, the adult trout of Lake Pontchartrain were not dependent upon the pinfish as in the case of the Florida trout. Instead, it appeared that the young Louisiana speckled trout partially substituted schizopods and bottom-living amphipods for the caridean shrimp and began to exploit at an early age the enormous populations of anchovies and larval fishes which inhabit the lake. In addition, the Louisiana population essentially bypassed the penaeid shrimp stage, achieving the adult diet by a length of 100 mm. rather than 150 mm. as in the Florida population.

Actually, the food of the young and adult trout indicated that in Lake Pontchartrain, neither is critically associated with shallow grassy areas. The presence of such forms as *Palaemonetes* sp. and the tanaid (*Leptochelia rapax*) did indicate some association of the young with grassy shallows, but the presence of quantities of schizopods and bottom-living amphipods is taken as evidence of feeding outside of the shallow flats. Stomachs of adults also contained some *Palaemonetes* sp. as well as bits of grass. The anchovies, however, which constituted the bulk of the adult food, are ubiquitous in the lake, and neither these nor the young croakers and penaeid shrimp give much indication of feeding habitat. Positive evidence that adult speckled trout feed in the deeper areas stems from the centers of successful sport-fishing activity, aimed primarily at obtaining this species. Using shrimp or small croakers as bait, fishermen regularly obtain this trout by trolling in deeper waters and by still-fishing around the wooden pilings of the railroad bridge which crosses the eastern neck of the lake.

Gunter (1945) pointed out a relationship between the availability of shrimp and the utilization of these crustaceans as food by the speckled trout. He found shrimp to be the predominant food in Texas during the summer months and noted a shift from shrimp to fishes (*Mugil* sp.) when shrimp suddenly became scarce following a January freeze. In line with Gunter's observations, Moody (1950) demonstrated that in Florida during the spring and summer months fishes and crustaceans contributed about equally to the diet of the adult speckled trout, whereas during the winter months fishes were about three times as important as crustaceans. This did not occur, however, in the Lake Ponchartrain series. Although all speckled trout over 150 mm. which were analyzed for food were taken during the warm months (March-September), fishes greatly predominated in the

diets. This again seems to point to the great availability of small fishes as opposed to penaeid shrimp in the muddy Louisiana waters.*

Leiostomus xanthurus Lacépède. Spot

The food of the spot has been reported by Linton (1904), Smith (1907), Welsh and Breder (1923), Hildebrand and Schroeder (1928), Hildebrand and Cable (1930), Gunter (1945), Roelofs (1954), and Reid (1954, 1955b). These investigators have analyzed spots of different sizes from various parts of their geographical range and have accumulated a long list of food items. In general, the smallest spots have been found to feed upon planktonic or benthonic microcrustaceans including chiefly copepods, ostracods, and amphipods. Adults have been shown to be bottom feeders, specializing upon small mollusks, polychaetous annelids, and small crustaceans. Occasional items encountered in the stomachs of the spots have included foraminifera, nematodes, chironomid larvae, mysids, shrimp, mites, small crabs, sea urchin spines, bryozoa, small fishes and fish scales, diatoms and other algae, vegetable debris, "grass", seaweed, and sand. Quantities of detritus and undetermined organic matter have consistently been encountered in the stomachs of all sizes, but have been especially prominent in the food of the adults.

Among the spots examined from Lake Pontchartrain, the smallest individuals contained three percent rotifers and schizopods, and this material may represent the vestiges of an earlier plankton-straining stage. These forms were virtually absent in the larger-sized fish (Table 9 and Fig. 10).

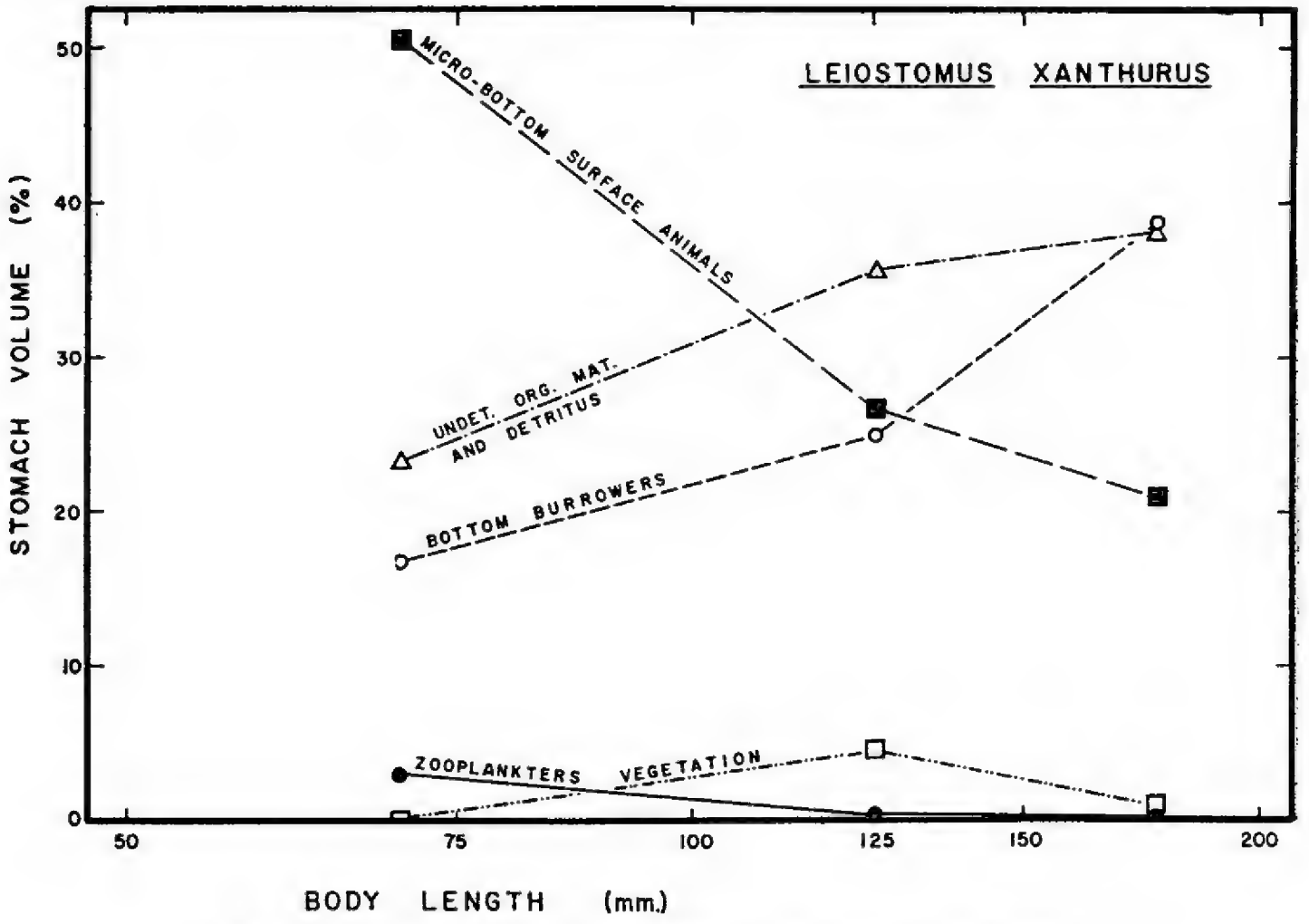

FIG. 10. Ontogenetic food progression of *Leiostomus xanthurus*.

* It appears to be a habit of the speckled trout to regurgitate the stomach contents at intervals following a meal. On such occasions a putrid mass of partially-digested fish appears on the surface surrounded by a small round oil slick. Commercial fishermen familiar with this habit frequently locate their quarry by the appearance and characteristic "fishy" odor of these oil spots. The low percentages of stomachs with food given in the literature undoubtedly reflect, in part, this phenomenon.

TABLE 9

Occurrence of food items in digestive tracts of 88 *Leiostomus xanthurus*

FOOD ITEMS	40.0–99.0 mm. 22 examined 18 with food		100.0–149.0 mm. 38 examined 28 with food		150.0–203.0 mm. 28 examined 20 with food	
	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume
Rotifera	9.1	2.0	.....	.....	.....	.....
Ostracoda	40.9	13.2	15.8	0.6	3.6	0.3
Copepoda (undet.)	13.6	6.2	2.6	.....	3.6	T
Harpacticoid	63.6	11.3	13.2	0.7	.....	.....
Mysid shrimp	4.5	1.0	7.9	0.3	.....	.....
Isopoda	31.8	7.6	44.7	9.0	35.7	11.8
Amphipoda	31.8	7.8	42.1	10.3	32.1	7.0
Cirripedia	.....	.....	.....	.....	3.6	.....
Insecta						
Coleoptera	.....	.....	13.2	0.5	.....	.....
Diptera	22.7	1.3	44.7	1.3	50.0	9.0
Arachnida	4.5	1.0	2.6	.....	.....	.....
Annelida	4.5	2.0	.....	.....	.....	.....
Mollusca						
Rangia cuneata	68.2	13.5	60.5	23.7	46.4	29.7
Mytilopsis leucopheata	.....	.....	2.6	.....	.....	.....
Gastropoda	50.0	4.0	31.6	5.5	30.0	1.9
Hydroids	4.5	.....	2.6	0.1	.....	.....
Foraminifera	27.3	0.5	7.9	0.1	.....	.....
Vertebrata						
Fish remains	.....	.....	15.8	8.4	3.6	.....
Algae—filamentous	4.5	.....	5.3	.....	14.3	0.3
Vascular Plants	4.5		7.9	4.5	14.3	0.6
Organic mat. (undet.)	63.6	26.5	52.6	20.6	67.8	19.0
Detritus	68.2	0.5	47.4	6.7	35.7	19.2
Sand	31.8	1.5	39.5	8.4	10.7	0.6
SUMMARY						
Rotifera, Copepoda, Ostracoda, Mysid shrimp		33.7		1.6		0.3
Gastropoda, Foraminifera		4.5		5.6		1.9
Isopoda, Amphipoda		15.4		19.3		18.8
Rangia cuneata		13.5		23.7		29.7
Misc. Invertebrates, Vertebrates		4.3		10.3		9.0
Vegetation		0.0		4.5		0.9
Incidental, Undet.		28.5		35.7		38.8

* Stomach and intestine included.

A number of small invertebrates grouped together as micro-bottom surface animals, made up over one-half of the food volume of the smallest spots. These species declined somewhat in importance in the larger fish, and constituted only one-fifth of the food of the largest spots. Included among the micro-bottom surface animals were ostracods (in heavy concentrations), copepods (primarily harpacticoids), isopods, amphipods, minute gastropods, and foraminifera. All these species presumably could have been either scooped from the bottom surface or strained from the immediately overlying layer of water.

Another group of small invertebrates consumed in quantity by the spot included the bottom-burrowers, animals which could be obtained only by digging into the bottom surface material. These forms made up only 17 percent of the food of the smallest size group, but they increased in importance in the food of the larger spots and constituted 39 percent of the material consumed by the largest individuals. Included among the

bottom-burrowers were large numbers of the clam (*Rangia cuneata*) and smaller quantities of chironomid larvae and annelids.

Undetermined organic material and detritus made up a considerable proportion of the food of spots of all sizes, and this material increased from 27 percent of the food volume in the smallest fish to 38 percent in the largest. The high percentage of this material in the diet of the spot is associated with the bottom habitat of the fish, and the increase in percent consumption of this matter by larger individuals parallels the increase in consumption of bottom-burrowers.

The stomach contents indicated that individuals occasionally specialize temporarily upon one food or another. A single stomach contained 250 harpacticoid copepods and five chironomids, another contained 200 amphipods, still another adult spot had 76 unbroken *Rangia cuneata* in its stomach. Most fishes, however, and especially those in the small and intermediate size categories, contained a variety of foods indicating more of a straining or sifting process than selective capture of individual animals.

Filamentous green algae including *Cladophora* sp., *Rhizoclonium* sp. and others, were encountered in one-tenth of the stomachs. Some vascular plant matter (probably *Vallisneria spiralis*) was found in the stomachs of eight individuals, one of which was packed with this material. The presence of this vegetation in the diet of the spot suggests some shallow water feeding. Most of the amphipods encountered were gammarids, but species of *Corophium* which were so abundant in the grassy shallows appeared to be entirely absent from the stomachs. Many of the invertebrate species which were abundant in the food of the spot appear to be inhabitants of the deeper waters indicating that this fish, in its feeding, utilizes such areas to a large extent. The presence of large quantities of detritus and the virtual absence of sand suggests that the species feeds largely on mud rather than on sandy bottoms. At least 6 species of minute gastropods were encountered, and the distributional patterns of these may eventually be employed to pinpoint the feeding grounds of the spot.

The spot appears to consume a limited amount of material throughout the morning and early afternoon. An increase in feeding intensity apparent in the late afternoon points to the fact that this fish may feed primarily at twilight or during the night hours (Fig. 11).

Hildebrand and Cable (*op. cit.*) pointed out that the very young spots tend to swim in schools and that a number of changes take place when the fish reach a length of ap-

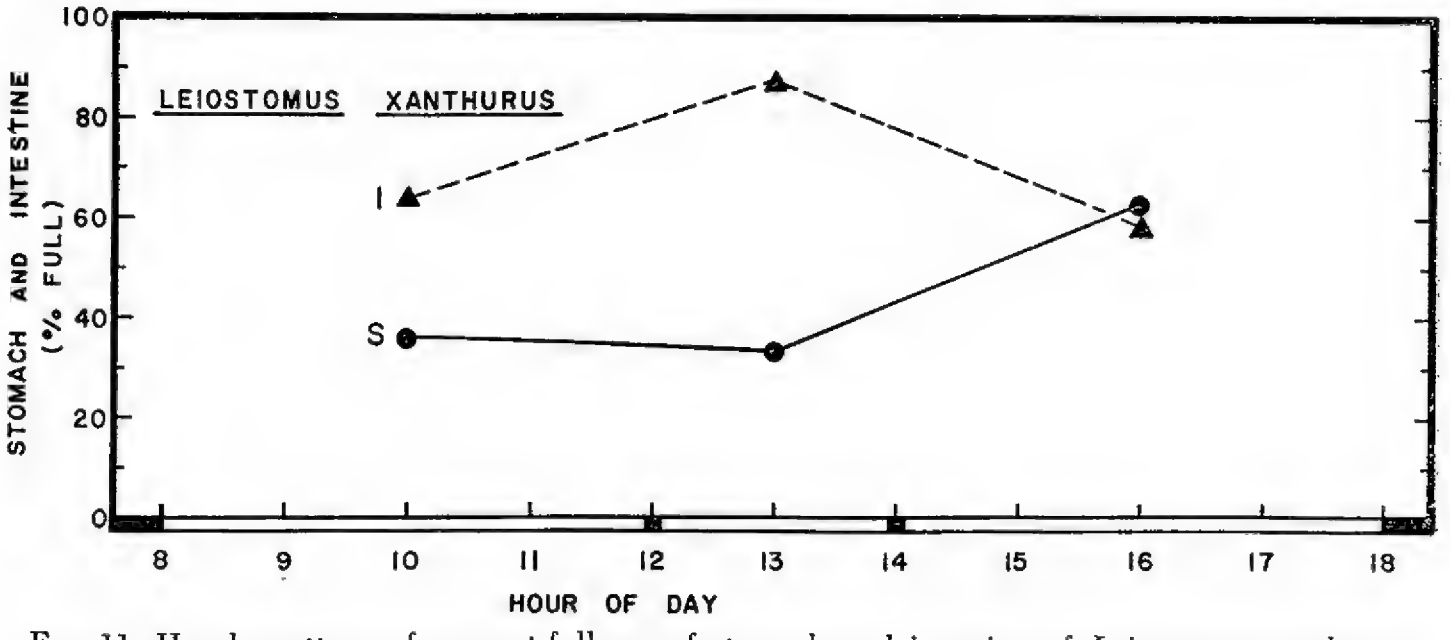

FIG. 11. Hourly pattern of percent-fullness of stomach and intestine of *Leiostomus xanthurus*.

proximately 25 mm. At about this size the schools break up, the oblique terminal mouth becomes inferior, and the food emphasis shifts from microcrustaceans to bottom material. Roelofs (1954) observed that in laboratory aquaria spots obtained food by making shallow dives to the bottom and scooping up mouthfuls of bottom material. Examining the gill structure of the spot he found that the alternating gill rakers and numerous fine setae comprise an excellent straining device for filtering small food particles from the water.

The accumulated evidence suggests that, as a rule, young spots feed just above the bottom. With increasing size they begin to feed more upon bottom surface animals, and as they approach maturity they dig more deeply into the bottom, taking a greater quantity of burrowing forms. Bottom detritus has been shown to be consumed in quantity by spots in North Carolina and Texas. In Lake Pontchartrain this material constitutes a substantial portion of the diet of spots of all stages, and it is particularly pronounced in the food of the larger, bottom-feeding stages. Temporary specialization upon one or another type of food has been reported, but most stomachs contain a wide variety of food items.

Micropogon undulatus (Linnaeus). Atlantic Croaker

The food of the Atlantic croaker on the south Atlantic and Gulf coasts has been investigated by Linton (1904), Smith (1907), Welsh and Breder (1923), Hildebrand and Schroeder (1928), Pearson (1929), Hildebrand and Cable (1930), Gunter (1945), McLane (1948), Roelofs (1954), Reid (1955b), and Reid, Inglis, and Hoese (1956). These workers succeeded in compiling an extensive list of food items recognized in the stomachs of croakers, which may be summarized as follows: mollusks (including pelecypods and gastropods), annelids, small crustaceans (copepods, ostracods, barnacle larvae, and amphipods), schizopods, mud shrimp, penaeid shrimp, crabs, bryozoans, sea urchin remains, hemichordates, tunicates, fishes (menhaden, threadfin shad, anchovies, small croakers, and gobies), unidentified fish vertebrae, diatoms, and incidental sand. It was observed that small croakers feed largely upon planktonic crustaceans and small bottom invertebrates, whereas the adults consume larger invertebrates such as annelids, clams, shrimp, and crabs as well as small fishes. Several of the workers reported the presence of large quantities of indeterminable matter and organic debris, especially among the young and medium-sized croakers. However, due to the general complexity of the food habits of this species and to geographic and seasonal differences in availability of the various acceptable items, the food relations of the Atlantic croaker have not been clearly understood to date.

In view of the obvious ecological success of the croaker in Lake Pontchartrain as evidenced by its large populations, widespread distribution, and year-around habitation of the lake (see Suttkus, 1954), and because of its importance as a food and game fish in the area, it was given special attention. Zooplankton, including calanoid copepods and a few schizopods, made up almost 70 percent of the food of the smallest size class (Table 10 and Fig. 12). This material decreased by about one-half in each succeeding size group, and in croakers of about 100 mm. zooplankton formed an insignificant portion of the diet. Clearly the food of the young croaker is the calanoid copepod (especially *Arcartia tonsa*), and whereas most stomachs contained less than 40 copepods, three small individuals contained more than 125 copepods apiece.

Small bottom-inhabiting animals comprised the chief food of the 25–50 mm. group.

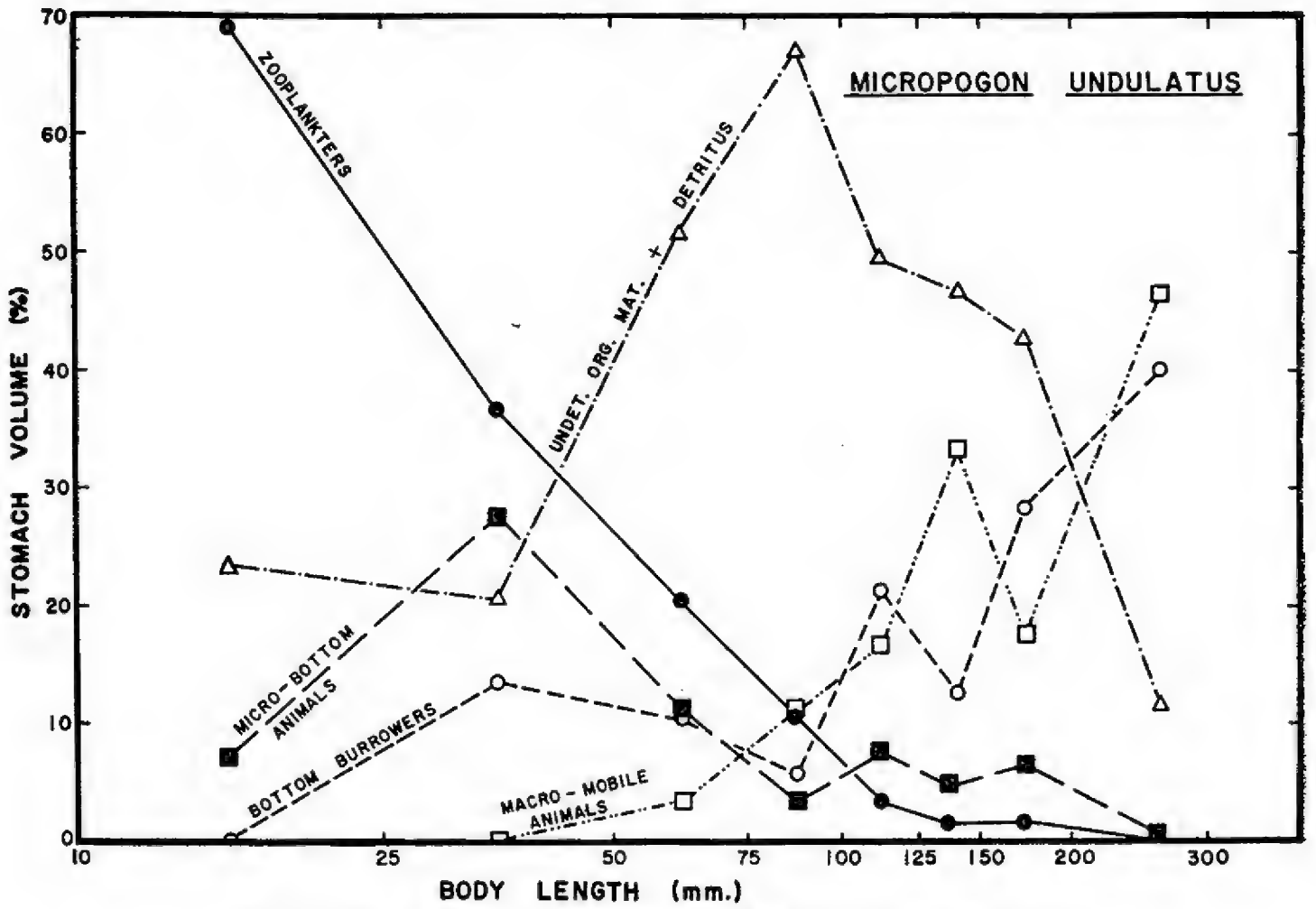

FIG. 12. Ontogenetic food progression of *Micropogon undulatus*.

These forms included both bottom-surface animals (harpacticoid copepods, amphipods, isopods, ostracods, minute snails, foraminiferans, and occasional coleopterans), as well as certain forms which have a greater tendency to burrow (chironomid larvae and small clams with attached mussels). Some of these bottom animals were present to a very limited extent in the smallest croakers, but they reached a peak of abundance (about 43 percent) in the 25–50 mm. size class and were present in reduced volume throughout all of the larger size groups. Occasionally the young, bottom-feeding croakers would specialize upon one form of food or another and contain up to 358 chironomids, or 10 mysids, or 46 amphipods. Most individuals in the intermediate size groups, however, exhibited a variety of food items, each present in small quantity as though general straining rather than selectivity were involved.

Detritus and undetermined organic material made up an important food category in croakers of all sizes, and this material was especially significant in croakers 50 to 200 mm. in length where it constituted over 40 percent of the stomach contents of each size group. In the 75–100 mm. group this material comprised over two-thirds of the food volume, and a decline in the utilization of this substance by the larger croakers was evident. No marked difference was noted between the detritus encountered in the stomachs of the croakers and that encountered in the stomachs of the spots. In both cases the material appeared to contain bits of shredded tissue, was sometimes flocculent in consistency, and was often greenish to dark brown in color. Furthermore, although much of the identifiable detritic material appeared to be of vegetable nature, it was generally impossible to distinguish between decomposed matter of animal and plant origin.

In the larger size groups the croaker was found to be a somewhat selective feeder, depending more upon the sorting or capture of larger discrete animals than upon filtra-

TABLE 10

Occurrence of food items in digestive tracts of 176 *Micropogon undulatus*

FOOD ITEMS	10.0–24.0 mm.		25.0–49.0 mm.		50.0–74.0 mm.		75.0–99.0 mm.		100.0–124.0 mm.		125.0–149.0 mm.		150.0–199.0 mm.		200.0–325.0 mm.	
	17 examined 15 with food		26 examined 26 with food		20 examined 20 with food		14 examined 10 with food		30 examined 28 with food		25 examined 24 with food		21 examined 18 with food		23 examined 19 with food	
	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume
Ostracoda	.....	.....	15.4	0.1	10.0	0.1	.....	.....	6.7	.....	12.0	T	4.8	.....	.....	.....
Copepoda (undet.)	.....	.....	3.8	.....	.....	.....	.....	.....	16.7	0.2	.....	.....	.....	.....	.....	.....
Calanoid	82.3	52.3	69.2	24.4	35.0	4.5	7.1	0.1	6.7	0.1	4.0	0.1	.....	.....	.....	.....
Harpacticoid	29.4	0.2	50.0	2.1	20.0	0.2	.....	.....	10.0	0.2	.....	.....	.....	.....	.....	.....
Mysid shrimp	23.5	16.9	19.2	12.2	30.0	16.1	21.4	10.5	40.0	3.3	24.0	1.4	14.3	1.8	8.7	T
Isopoda	5.9	5.1	11.5	1.9	30.0	0.6	21.4	2.1	30.0	2.4	24.0	0.1	28.6	2.2	.....	.....
Amphipoda	17.6	1.8	57.7	23.2	50.0	9.9	7.1	1.3	43.3	2.3	40.0	3.7	23.8	4.3	.....	.....
Palaemonid shrimp	.....	.....	.....	.....	.....	.....	.....	.....	3.3	2.4	4.0	.....	4.8	.....	.....	.....
Penaeus sp.	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	4.8	0.4	.....	.....
Crabs (undet.)	.....	.....	.....	.....	.....	.....	21.4	1.8	.....	.....	4.0	0.2	14.3	1.7	8.7	4.2
Rithropanopeus harrisii	.....	.....	.....	.....	.....	.....	.....	.....	20.0	7.3	24.0	8.2	28.6	11.4	26.1	11.8
Callinectes sapidus	.....	.....	.....	.....	.....	.....	.....	.....	3.3	0.6	16.0	9.5	.....	.....	21.7	8.2
Insecta	.....	.....	3.8	.....	.....	.....	7.1	0.3	20.0	0.4	4.0	.....	.....	.....	4.3	.....
Coleoptera	.....	.....	.....	.....	5.0	0.2	.....	.....	23.3	2.5	32.0	1.0	.....	.....	.....	.....
Diptera	5.9	.....	50.0	15.1	65.0	9.8	50.0	1.5	56.7	5.8	56.0	11.6	19.0	2.5	13.0	0.2
Annelida	.....	.....	.....	.....	.....	.....	.....	.....	40.0	15.0	8.0	0.5	4.8	0.2	4.3	0.8
Mollusca																
Rangia cuneata	.....	.....	7.7	.....	10.0	0.6	42.9	4.2	30.0	0.1	52.0	0.3	42.9	5.5	52.2	29.4

Mytilopsis leucopheata	.....	.....	.....	.....	.....	.....	7.1	.....	3.3	.....	12.0	0.3	19.0	20.3	39.1	9.7
Gastropoda	.....	.....	.....	.....	5.0	0.2	.....	.....	.....	.....	.....	.....	4.8	.....	8.7	0.8
Hydroids	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	8.0	.....	.....	.....	4.3	.....
Sponges	.....	.....	.....	.....	.....	.....	.....	.....	3.3	0.2	.....	.....	.....	.....	.....	.....
Foraminifera	5.9	0.1	7.7	0.3	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Vertebrata																
Anchoa mitchilli	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	4.0	2.7	4.8	1.3	4.3	2.0
Cyprinodon variegatus	.....	.....	.....	.....	.....	.....	.....	.....	3.3	1.6	.....	.....	.....	.....	.....	.....
Gambusia affinis	.....	.....	.....	.....	.....	.....	.....	.....	3.3	1.1	.....	.....	.....	.....	.....	.....
Gobiosoma bosci	.....	.....	.....	.....	.....	.....	7.1	9.1	.....	.....	4.0	4.5	.....	.....	.....	.....
Micropogon undulatus	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	4.3	9.2
Myrophis sp.	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	4.3	9.4
Syngnathus sp.	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	4.0	1.8	4.8	1.3	.....	.....
Fish remains	.....	.....	.....	.....	5.0	3.3	14.2	T	13.3	3.5	12.0	6.5	14.3	1.5	4.3	1.4
Algae—Filamentous	.....	.....	.....	.....	.....	.....	.....	.....	3.3	0.2	8.0	.....	9.5	0.4	13.0	0.2
Vascular plants	.....	.....	.....	.....	.....	.....	.....	.....	16.7	1.9	20.0	0.4	28.6	2.3	8.7	T
Eggs and Cysts	5.9	0.3	3.8	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Organic mat. (undet.)	58.8	23.2	61.5	16.3	80.0	43.3	85.7	40.5	83.3	35.1	88.0	41.9	71.4	36.0	52.2	8.9
Detritus	11.8	.....	65.4	4.3	90.0	8.7	71.4	26.5	43.3	14.1	60.0	4.7	47.6	6.6	65.2	2.8
Sand	.....	.....	26.9	0.2	15.0	2.2	35.7	1.8	.....	.....	12.0	0.2	14.3	.....	8.7	.....

SUMMARY

Copepoda	52.5		26.5		4.7		0.1		0.5		0.1		0.0		0.0
Mysid shrimp	16.9		12.2		16.1		10.5		3.3		1.4		1.8		0.0
Isopoda, Amphipoda	6.9		25.1		10.5		3.4		4.7		3.8		6.5		0.0
Insecta	0.0		15.1		10.0		1.8		8.7		12.6		2.5		0.2
Mollusca	0.0		0.0		0.8		4.2		0.1		0.6		25.8		39.9
Fishes	0.0		0.0		3.3		9.1		6.2		15.5		4.1		22.0
Crabs, Shrimp	0.0		0.0		0.0		1.8		10.3		17.9		13.5		24.2
Miscellaneous	0.1		0.4		0.1		0.0		17.3		0.9		2.9		1.0
Incidental, undet.	23.5		20.8		54.2		68.8		49.2		46.8		42.6		12.9

* Stomach and intestine included.

tion of microscopic creatures or consumption of detritus. This trend of selectivity becomes progressively more noticeable above 100 mm., and in croakers above 200 mm. larger animals constituted over 85 percent of the total food volume. Among the animals consumed by adult croakers the following made up significant percentages in some size classes: annelids, up to 15 percent in one class, palaemonid and penaeid shrimp made up less than 3 percent in any of the adult classes, crabs (*Callinectes sapidus* and *Rithropanopeus harrisii*) up to 20 percent, mollusks (chiefly the clam, *Rangia cuneata*) up to 40 percent, and small fishes (including *Anchoa mitchilli*, *Cyprinodon variegatus*, *Gambusia affinis*, *Gobiosoma bosci*, young *Micropogon undulatus*, *Myrophis* sp., *Syngnathus* sp., and remains of other species) up to 22 percent. Undoubtedly, size is an important factor determining the utilization of a particular food item by the adult croaker, and even young croakers as large as 67 mm. are not free from predation by adults over 300 mm. in length. Miscellaneous items encountered in the stomachs of some croakers included sponge, hydroids, eggs and cysts, worm burrows, adult insects, filamentous algae (*Cladophora* sp.), and sand.

On the basis of the above information it is clear that, whereas the croakers of Lake Pontchartrain consume a great variety of different food items, from young to adult they pass through a succession of four overlapping, but distinctly recognizable food stages. They specialize successively upon (1) zooplankton, (2) micro-bottom animals, (3) detritus, and (4) larger animals, the latter group including burrowers, crawlers, and swimmers.

As a rule, small croakers displayed only one or two types of food within a given stomach with little variation from one croaker to the next. Intermediate-sized individuals, however, feeding upon small bottom invertebrates exhibited a wide variety of foods within any given stomach, and differences between one individual and another were common. Adults, as a group, continued to display a varied diet, but since the food items consumed were individually much larger, the variety of items within a given stomach tended to decrease.

Study of the percent fullness of the stomachs and intestines reveals a clear picture of the daily pattern of feeding of the young and adult croakers (Fig. 13). In the young plankton-feeding and bottom-browsing individuals (11.5–74 mm.) feeding intensity is low during the early morning and increases to a peak by early afternoon which gradually tapers off toward evening. This may be related to a presumed vertical migratory pattern of the calanoid copepods which constitute a major element of the diet of these small croakers. Presumably, during the hottest and lightest portion of the day these copepods would be most concentrated near the bottom, and, therefore, most available as food for the young fishes. Intermediate-sized croakers (75–150 mm.) which feed upon detritus together with a general mixture of animals from the bottom water and bottom surface appeared to feed moderately throughout the day, increasing their feeding activity somewhat toward evening (the dip in the curve during the late afternoon appears to be an artifact resulting from small numbers in that particular time class). Large adult croakers (150–325 mm.) exhibit two distinct feeding periods during the day. An early peak in mid-morning is followed by a period of low feeding intensity throughout the afternoon with some indications of increased feeding activity toward the evening. This bimodality may be associated with periodic availability of its molluscan, crustacean, and vertebrate food, with its own necessity of escaping mid-day predation, or with general physiological inactivity during the warmest and lightest portions of the day.

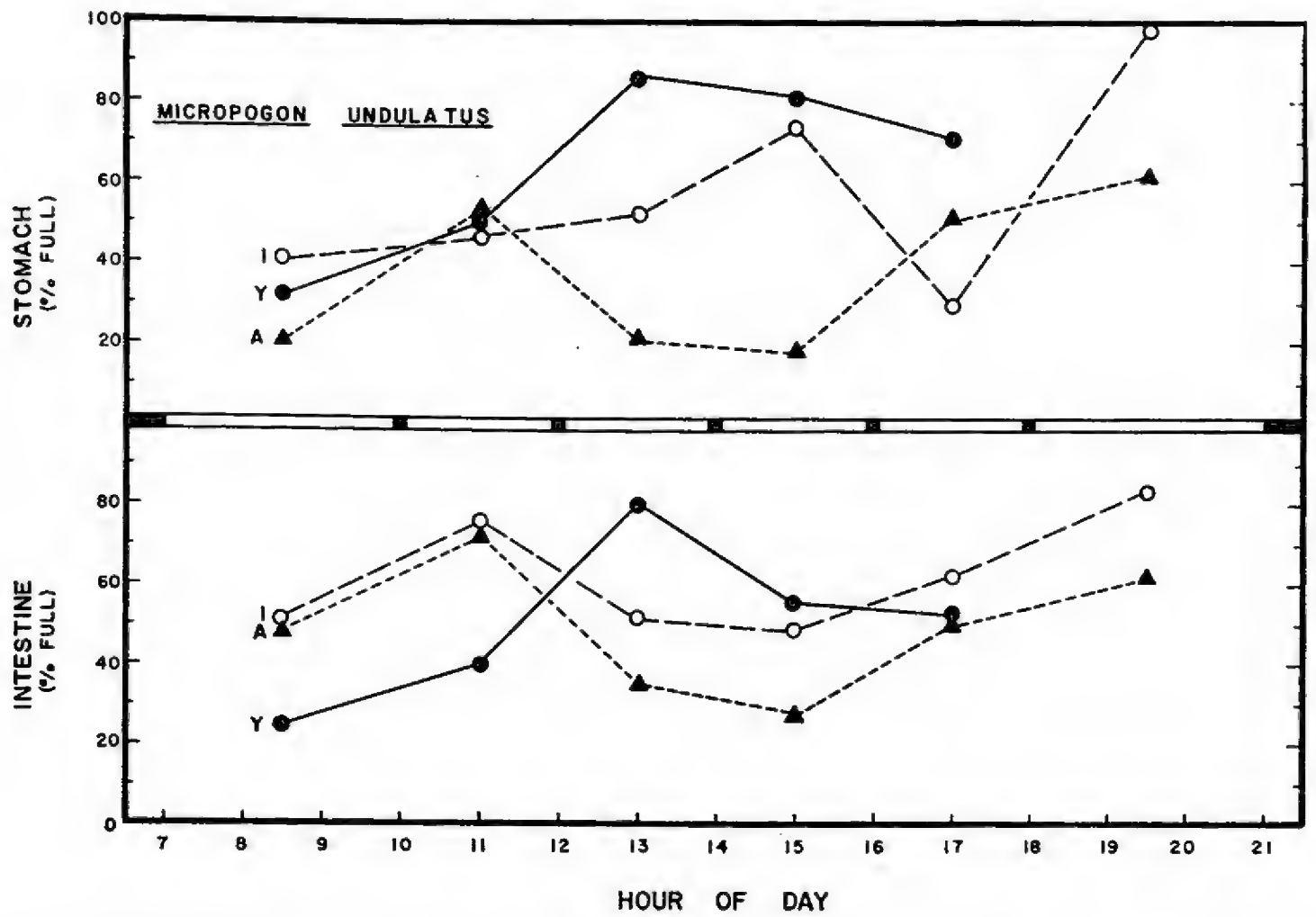

FIG. 13. Hourly pattern of percent-fullness of stomach and intestine of *Micropogon undulatus* (young, intermediate, and adult).

Studies to date suggest that the food of the croaker is roughly similar throughout its geographic range, but local differences in detail may be pointed out. Along the Atlantic coast polychaetous annelids are of considerable importance as food, and quantities of echinoderms and some ascidians and hemichordates are consumed in that area. Along the Gulf coast these items appear to be of less importance, whereas quantities of shrimp, fishes, and crabs are substituted. On the Atlantic coast the staple food mollusk of the adult croaker appears to be the razor clam, which is replaced in Lake Pontchartrain by *Rangia cuneata* and *Congeria leucopheata*, and in east Texas by *Macoma mitchelli*. Several investigators on the Atlantic coast have encountered quantities of debris or undeterminable organic matter in the stomachs of young and medium-sized croakers and have generally been inclined to consider such material as "incidental" or simply annelid or other large food digested beyond recognition. Reid (1955b), working in Texas, appears to have been the first to point out that organic debris may constitute an important energy source for the croaker as well as for other species of sciaenid fishes. This point is reemphasized by the food contents from Louisiana specimens.

Regarding adaptations of the croaker for obtaining its food, Welsh and Breder (1923) noted that this fish possesses a flattened profile and sensitive, pendant mandibular barbels typical of bottom feeders. Roelofs (1954) reported that when feeding in laboratory aquaria, croakers dive into the bottom with some force, digging as they feed, and thus they are able to obtain subsurface animals for food. He also studied the gill rakers of this fish, pointing out that they tend to be short and stout with relatively few setae. Hence, the gill structure of the adult croaker forms a coarse basket rather than a fine straining mechanism and tends to retain only the larger particulate matter. This knowledge aids in understanding the food habits of the species and in explaining the observed differences

between the food habits of the adult croaker and those of the adult spot. The croaker shovels more deeply while the spot scoops the surface; also, the latter retains what the former discards. As a matter of fact, although the adults of the two species appear not to be in keen competition for food, there does exist a great deal of overlap in the food of the intermediate-sized croaker and that of the adult spot.

Pogonias cromis (Linnaeus). Black Drum

Smith (1907) mentioned that the black drum is a bottom feeder taking mainly crustaceans and various mollusks including oysters. Welsh and Breder (1923) agreed, emphasizing depredations of the black drum upon oyster beds. Reporting on the food of 117 black drums (80–990 mm.) from Texas, Pearson (1929) found that young individuals (80–200 mm.) feed a great deal upon what he termed "soft foods" (including fish and annelids) as well as upon crustaceans and mollusks. With increasing size the "soft foods" were dropped from the diet, and older drums were found to feed largely upon mollusks (74 percent) and crabs (16 percent). The mollusks included mainly *Mulinia transversa corbuloides* with some *Mytilus* sp. and *Ostrea* sp.

Gunter (1945) examined the stomach contents of 124 black drums (205–460 mm.) from southern Texas, only 96 of which contained recognizable material. He found that crustaceans, molluskc, and fishes were the most abundant foods. The crustaceans included large numbers of amphipods, as well as blue crabs, penaeid shrimp, palaemonid shrimp (*Palaemonetes sp.*), pistol shrimp (*Cargo* sp.), and oyster crabs (*Panopeus* sp). The mollusks included small gastropods, and pelecypods (*Donax* sp. and razor clams), and the only identifiable fish was the goby (*Gobiosoma bosci*) which appeared in the stomachs of at least 12 individuals and which numbered as high as 23 in a single stomach. Reid (1955b) examined seven young black drums from East Bay, Texas, and in the six which contained food he found masses of pelecypod shell debris.

Among the small drums examined from Lake Pontchartrain, mollusks made up over 65 percent of the food material, and mud crabs (*Rithropanopeus harrisii*) made up about 12 percent (Table 11). A few other small invertebrates were noted. While the quantity of detritus present in the stomachs was very small, more than one-fifth of the food consisted of organic material which was not positively identifiable. This material frequently took on the appearance of a milky sludge and was probably composed of the partially-digested bodies and mucus of the many pelecypods consumed. Among the three large black drums examined, the stomach of one was empty while the remaining two were about half full of the clam (*Rangia cuneata*). In addition to the above, a number of large black drums were examined qualitatively in the field. These generally contained only the remains of *Rangia cuneata*, supporting the conclusion that all sizes of black drum above 100 mm. in length are primarily dependent upon this clam as the staple food while in Lake Pontchartrain. Welsh and Breder (1923) pointed out that the black drum exhibits the flattened profile and mandibular barbels typical of bottom-feeding fishes. Pearson (1929) correlated the food with the environment in which the fish feeds. He noted that the pelecypod food of the black drum (in this case, the clam, *Mulinia*) lives in shallow muddy lagoons and bays, and that the black drum is most abundant where the water is always turbid, highly saline to brackish, shallow (4ft.), and characterized by temperature extremes. Reid (1955a) mentioned that this species, like the redfish, *Sciaenops ocellata*, has a characteristic habit of grazing in the salt marshes when these marshes are under water.

Commercial fishermen have pointed out to the writer that black drums frequently dig for mollusks in shallow water, and in so doing they literally stand on their heads waving the caudal fins aloft. Where the water is very shallow the caudal fins may clear the surface and be visible for some distance. This phenomenon of "flagging frequently enables the commercial fisherman to locate the black drum among the marshes and tidal flats of the Louisiana coast. Apparently the phenomenon of head-standing is not limited to shallow waters. Mr. Percy Viosca, Jr. (in personal conversation and correspondence) has indicated that while flying over Lake Pontchartrain on a still summer day he noted on the surface what appeared to be the result of large black drums feeding singly or in groups through the western sector of the lake. Digging and flagging, each drum created an upwelling of turbid water resembling smoke pouring from a chimney. These fish were undoubtedly digging for the clam, *Rangia cuneata,* the only abundant large pelecypod in that area of the lake.

Indirect evidence indicates that the adult black drum can easily crush and discard the hard shells of adult rangia clams retaining only the soft bodies as food. In the field it was repeatedly observed that freshly-caught specimens with shell fragments in the buccal cavity contained only a milky mush in the stomach. Although a number of authors have noted shell fragments occurring in the stomach of this fish, such material appears to have been derived from small or more fragile mollusks.

It is generally accepted that the black drum is a bottom feeder, but details of the food habits of the species are still poorly known. Individuals less than 100 mm. have not been well investigated, and larger individuals have generally been lumped into a single group. On the basis of the existing knowledge of the food habits of the species two feeding stages are distinguishable, and from what is known of related sciaenids, a third may be postulated. The very young undoubtedly feed upon planktonic or bottom-dwelling mi-

TABLE 11

Occurrence of food items in digestive tracks of 24 *Pogonias cromis*

	116.0–218.0 mm.	
	24 examined 20 with food	
FOOD ITEMS	Percentage of tracts* containing item	Percentage of total stomach volume
Isopoda	8.3	0.4
Amphipoda	4.2	.....
Crabs		
Rithropanopeus harrisii	20.8	12.2
Insecta		
Dipter—larvae	16.7	0.1
Mollusca		
Rangia cuneata	75.0	55.5
Mytilopsis leucopheata	12.5	9.9
Gastropoda	20.8	0.1
Fish scales	4.2	.....
Algae—filamentous	4.2	
Organic mat. (undet.)	41.7	21.7
Detritus	41.7	T
Sand	12.5	.....
SUMMARY		
Crabs		12.2
Mollusks		65.5
Misc. Invertebrates		0.5
Organic mat. (undet.)		21.7

* Stomach and intestine included.

crocrustaceans. Following this stage, larger bottom invertebrates must enter the diet, individuals within the 100–200 mm. class being dependent primarily upon small mollusks, crustaceans, and "soft foods" (fish and annelids). Larger individuals (over 500 mm.) subsist chiefly upon mollusks. In Lake Pontchartrain the primary food of the middle-sized as well as the adult black drums, appears to be the clam, *Rangia cuneata.*

Sciaenops ocellata (Linnaeus). Red Drum, Redfish

The food of the redfish on the Atlantic coast has been reported by Linton (1904) and Hildebrand and Schroeder (1928), and food habits of this species on the Gulf coast of Texas have received the attention of Pearson (1929), Gunter (1945), Knapp (1949), and Reid (1955b). The smallest redfishes examined (30 mm. and over) have been found to consume small crustaceans such as schizopods and amphipods. Food of the larger size groups has been found to include primarily penaeid shrimp (*P. aztecus* and *P. setiferus*), blue crabs (*Callinectes sapidus*) and fishes (*Brevoortia* sp., *Galeichthys felis, Anchoa mitchilli, Cyprinodon variegatus, Fundulus* sp., *Lucania parva, Mugil cephalus, Menidia* sp., *Syngnathus* sp., *Leiostomus xanthurus, Lagodon rhomboides, Symphurus plagiusa, Gobiosoma bosci,* and *Myrophis punctatus,* as well as a number of unidentified species). In addition, a variety of other organisms has been encountered in the stomachs of large redfish with less frequency. These include the following: bivalves, squids, annelids, crustaceans including grass shrimp (*P. vulgaris*), mud crabs (*Neopanope t. texana,* and *Panopeus herbstii*), snapping shrimp (*Crago* sp.), mud shrimp (*Callianassa jamaicense louisiananum*), a large marsh rat, algae, and vascular plant matter.

Stomach contents of 17 redfish (184–625 mm.) from Lake Pontchartrain were examined. Among the 12 which contained recognizable food, crabs predominated and included both the blue crab (*Callinectes sapidus*) and the mud crab (*Rithropanopeus harrisii*) which together made up 62 percent of the food. Other important categories included fish remains (17 percent) and unidentified organic material (15 percent). Vascular plants made up five percent of the stomach contents, and amphipods, palaemonid shrimp, and hydroids constituted less than one percent each. Within the above size range, large living invertebrates and fishes made up four-fifths of the material consumed by the redfish, and especially heavy predation upon blue crabs was indicated.

Available information indicates that young redfish subsist mainly upon a diet of small crustaceans including amphipods and schizopods, with larger individuals shifting to larger crustaceans and fishes. In inside waters, as pointed out by Gunter (*op. cit.*) and borne out in the Pontchartrain series, the principal food of the adult redfish is the blue crab, whereas in marine waters penaeid shrimp achieve greatest significance. In both habitats a wide variety of different invertebrates is utilized as supplementary food. As pointed out by Pearson (*op. cit.*) and Gunter (*op. cit.*) this predatory fish consumes both bottom-living and free-swimming forms, and the former author noted that in its feeding habits the redfish is intermediate between the bottom-feeding black drum and the pelagic predator, the speckled trout. It has been reported by Reid (1955a) that the redfish, like the black drum, frequently grazes in flooded salt marshes, a habit which appears to be of considerable significance in the ecology of the species in the marshy areas of southeastern Louisiana.

SPARIDAE

Archosargus oviceps Ginsburg. Gulf Sheepshead

In 1894 Brooks discussed the food of the sheepshead, and on the basis of personal observations concluded that although this fish browses among algae, its food is "ex-

clusively animal", including barnacles and young oysters. Linton (1904) examined the stomach contents of two specimens and found crustaceans (including hermit crabs), sea urchin fragments, shells, and gorgonian spicules. Smith (1907) mentioned that the sheepshead feeds chiefly upon mollusks and crabs, a statement which was repeated by Hildebrand and Schroeder (1928) apparently without further verification. Gunter (1945), however, examined the food of 18 specimens (190–365 mm.) from southern Texas, and he found that in most individuals the long guts were distended with great quantities of plant material ("grass" and algae). Crabs (including *Callinectes sapidus*), gastropods, and unidentified shells were encountered in only a few individuals. Gunter concluded, therefore, that regardless of previous statements, the adult sheepshead is largely herbivorous. Gunter (1954) later reported observing the clumsy but successful attack by an adult sheepshead on a half grown blue crab swimming at the surface.

Viosca (1954) drawing upon years of personal experience indicated that in Louisiana the sheepshead feeds both upon "grass" in the beds of aquatic vegetation and upon small invertebrates inhabiting oyster reefs and other hard surfaces. As invertebrate food items, he listed sessile forms such as barnacles, mussels, small oysters, and hydroids, as well as small mobile species including crabs, shrimp, and snails. Reid, Inglis, and Hoese (1956) stated that four sheepshead (230–400 mm.) from East Bay, Texas had consumed crabs, pelecypods, and vegetable matter.

In the present study 11 specimens of the gulf sheepshead (218–410 mm.) from Lake Pontchartrain were analyzed, and all contained identifiable food. Vegetation was the most abundant material encountered and included filamentous algae (*Cladophora* sp.) together with vascular plants (*Vallisneria spiralis* and *Ruppia maritima*) which constituted over 54 percent of the stomach volume. Invertebrates included mussels (*Congeria leucopheata* and *Mytilus recurvus*) 19 percent, clams (*Rangia cuneata*) 8 percent, sponge (*Spongilla l, lacustris*) 10 percent, and mud crabs (*Rithropanopeus harrisii*) 1.5 percent. Young croakers and remains of other small fishes constituted three percent of the food, and blue crabs (*Callinectes sapidus*), amphipods, isopods, barnacles (*Balanus* spp.), small gastropods, and hydroids made up less than one percent each. A small quantity of undetermined organic material also was present.

The food of young sheepshead apparently has not been investigated. Larger individuals employ the well-formed, incisor-like teeth for cropping vegetation, for picking up small active invertebrates, and for scraping sessile animals from hard surfaces. The sheepshead's habit of nibbling the invertebrate epifauna from vertical posts and pilings appears to be widely recognized among sport fishermen of the Gulf area. Individuals collected from inshore shallows such as Lake Pontchartrain and the bays of southern Texas were found to have fed chiefly upon vegetation. This species is further remarkable in its occasional utilization of sponge as food.

Lagodon rhomboides (Linnaeus). Pinfish

Linton (1904) and Smith (1907) mentioned that the food of the pinfish is quite varied, including primarily mollusks, worms, crustaceans (amphipods and small shrimps and crabs), small fishes, and vegetation ("sea weed", "sea lettuce", and "vegetable detritus"). A variety of other animal remains also was present. Hildebrand and Schroeder (1928) found that the food of 13 specimens included (in decreasing order of abundance) vegetable debris, crustaceans, mollusks, and annelids. Gunter (1945) reported the food of eight large pinfish (150–285 mm.) from Texas. One fish had consumed razor clams, and the remaining individuals all contained plant material

including algae and "grass". Because of the stomach contents and the presence of large, incisor-like teeth, the pinfish was regarded by Gunter as being a "grazer". Reid (1954) provided information on the food of 65 young pinfish (15–128 mm.) from Florida. His data indicate that the smallest fish (15–50 mm.) fed most frequently upon copepods, amphipods, and shrimp. The next larger size group (51–100 mm.) contained (in decreasing order of occurrence) copepods, shrimp, organic detritus and mud, amphipods, mollusks, crabs, fishes, and plant detritus. The largest pinfish group (101–128 mm.) contained only copepods, amphipods, shrimps, and mollusks, each occurring in 18–25 percent of the stomachs. Although dealing primarily with smaller individuals, Reid's study seems to suggest that if invertebrates are sufficiently abundant, less vegetation is consumed by the pinfish.

In the Lake Pontchartrain study micro-bottom animals constituted the principal food of the two smallest size classes (40–64 mm. and 65–74 mm.), making up from 60 to 80 percent of the ingested material in each class (Table 12 and Fig. 14).

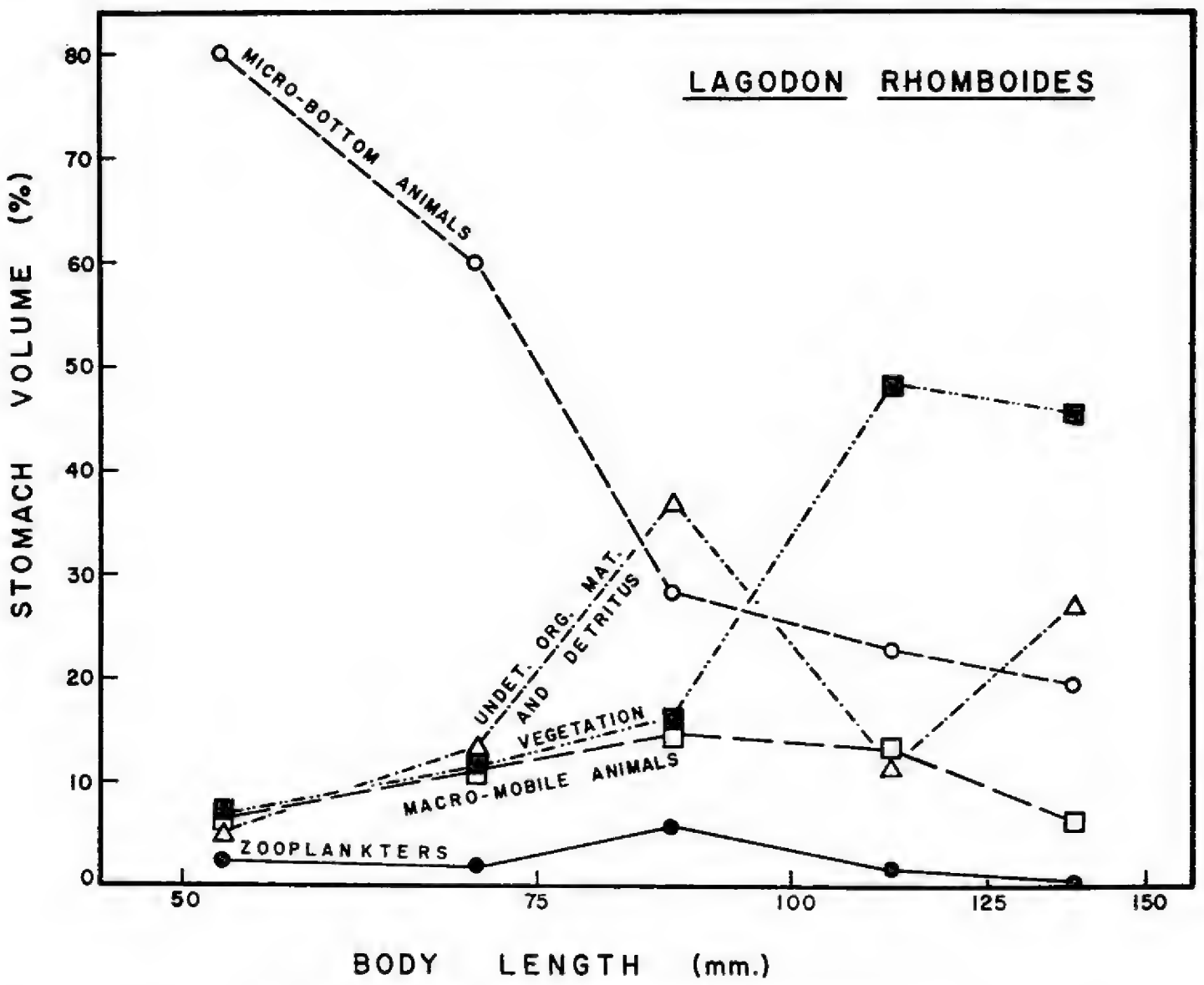

FIG. 14. Ontogenetic food progression of *Lagodon rhomboides*.

Bottom amphipods (including *Corophium* spp., *Cerapus* sp., and various grammarids) made up the bulk of this material. Also included were bottom sopepods, isopods, and dipteran (chironomid) larvae and pupae. Although larger pinfish concentrated primarily upon other food materials, micro-bottom animals continued to be consumed, and these forms made up 20–30 percent of the food volume in each of the upper size classes.

Pinfishes of all sizes consumed some vegetation. In the 40–64 mm. group this ma-

TABLE 12

Occurrence of food items in digestive tracts of 101 *Lagodon rhomboides*

FOOD ITEMS	40.0–64.0 mm. (20 examined, 20 with food)		65.0–74.0 mm. (21 examined, 21 with food)		75.0–99.0 mm. (25 examined, 24 with food)		100.0–124.0 mm. (20 examined, 19 with food)		125.0–150.0 mm. (15 examined, 15 with food)	
	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume
Ostracoda	.....	.....	.....	.....	.....	.....	5.0	.....	.....	.....
Copepoda (undet.)	.....	.....	4.8	0.1	4.0	0.2	.....	.....	.....	.....
Arguloid	5.0	0.3	4.8	0.3	.....	.....	.....	.....	.....	.....
Calanoid	.....	.....	4.8	0.3	.....	.....	5.0	.....	.....	.....
Harpacticoid	10.0	0.1	4.8	0.1	.....	.....	20.0	1.6	33.3	2.0
Mysid shrimp	5.0	2.4	19.0	1.6	28.0	5.8	10.0	1.8	13.3	0.6
Isopoda	25.0	0.3	42.9	2.2	48.0	2.7	40.0	2.8	60.0	3.2
Amphipoda	90.0	64.5	81.0	47.6	60.0	24.3	45.0	17.7	40.0	13.0
Palaemonetes sp.	.....	.....	.....	.....	.....	.....	5.0	3.4	.....	.....
Macrobrachium ohione	5.0	4.1	.....	.....	.....	.....	.....	.....	.....	.....
Crabs (undet.)	.....	.....	4.8	2.8	4.0	.....	10.0	1.4	.....	.....
Rithropanopeus harrisii	5.0	2.4	9.5	2.5	20.0	10.5	20.0	8.6	26.7	6.4
Callinectes sapidus	.....	.....	9.5	0.3	.....	.....	.....	.....	.....	.....
Insecta (Diptera)	50.0	12.0	33.3	10.6	20.0	0.5	15.0	0.3	20.0	0.9
Annelida	10.0	2.7	4.8	0.1	8.0	1.9	10.0	0.9	.....	.....
Mollusca										
Rangia cuneata	.....	.....	.....	.....	8.0	.....	.....	.....	.....	.....
Mytilopsis leucopheata	.....	.....	.....	.....	4.0	.....	.....	.....	6.7	0.5
Gastropoda	.....	.....	.....	.....	4.0	.....	.....	.....	.....	.....
Hydroids	.....	.....	.....	.....	16.0	1.1	.....	.....	.....	.....
Vertebrata										
Gobiosoma bosci	.....	.....	4.8	5.7	.....	.....	.....	.....	6.7	.....
Fish remains	10.0	.....	23.8	3.3	40.0	5.8	10.0	.....	.....	.....
Bottom Diatoms	5.0	0.1	.....	.....	.....	.....	10.0	0.1	6.7	0.2
Algae—filamentous	15.0	5.8	14.3	11.2	28.0	14.1	70.0	40.3	66.7	34.5
Vascular plants	.....	.....	4.8	0.2	16.0	2.3	40.0	8.0	53.3	11.1
Organic mat. (undet.)	80.0	2.8	90.5	6.9	84.0	20.0	40.0	7.8	40.0	18.9
Detritus	25.0	2.7	47.6	3.3	60.0	10.1	45.0	4.0	40.0	8.5
Sand	10.0	.....	9.5	.....	32.0	0.6	45.0	1.3	13.3	0.1
SUMMARY										
Microcrustacea (excl. Amphipoda)		3.1		4.6		8.7		6.2		5.8
Amphipoda		64.5		47.6		24.3		17.7		13.0
Diptera		12.0		10.6		0.5		0.3		0.9
Macrocrustacea		6.5		5.6		10.5		13.4		6.4
Fishes		0.0		9.0		5.8		0.0		0.0
Vegetation		5.8		11.4		16.4		48.3		45.6
Misc. Invertebrates		2.7		0.1		3.0		0.9		0.5
Incidental and Undet.		5.6		10.2		30.7		13.2		27.7

* Stomach and intestine included.

terial made up 6 percent of the food volume, and it increased thereafter so that in both groups over 100 mm., vegetation constituted almost half of the total food volume. Most of this vegetation was composed of filamentous green algae, especially *Cladophora* sp., although species of *Oedogonium*, *Rhizoclonium*, and *Spirogyra* were also represented. Vascular plants were of significance only in the two larger size classes where they constituted about 10 percent of the food volume. These included *Vallisneria spiralis* and probably also *Ruppia maritima*. There is no question of the algae being an "incidental" item in the food of this fish, although small invertebrates were frequently found entangled in the balls of filamentous algae.

A few zooplankters, including schizopods and planktonic copepods, were represented in the food of each size class. This material appeared in greatest abundance in the food of the intermediate-sized fish and dropped to less than one percent in the largest size class. Pinfish of all sizes also consumed some macro-mobile animals including crabs (*Callinectes sapidus* and *Rithropanopeus harrisii*), shrimp (*Palaemonetes* sp. and *Macrobrachium ohione*), and fishes (*Gobiosoma bosci* and others). Contrary to expectations, the macro-mobile animals achieved their most important food status in the intermediate size groups, and adult pinfish appeared to consume somewhat less of this material. Undetermined organic material and detritus seemed to be of little importance in the food of the smaller pinfish. This material, however, made up more than one-third of the food volume in the intermediate size group, decreasing somewhat in the larger individuals.

The Pontchartrain data indicate that small pinfish (50–75 mm.) consume primarily micro-bottom animals. In large pinfish (above 100 mm.) the primary food is filamentous algae. During the transition stage (75–100 mm.) there seems to be no specialization, and as though the fish were having difficulty obtaining enough to eat, increased volumes of detritus and decaying organic material were taken in. Zooplankton and macro-mobile animals were included to some extent in the food of all size classes.

The pinfish is a very selective feeder, and the number of different types of food items per stomach is generally small. With increasing size there does occur, however, a noticeable increase in the average number of identifiable types of food per stomach, from an average of 2.1 in the smallest size group to 3.1 in the largest. This increase is associated with the fact that small invertebrates often accompany the ingested filamentous algae. As indicated by Figure 15, both young and adult pinfish are daytime feeders, beginning in the morning and continuing to feed throughout the afternoon.

Gunter (1945) and Reid (1954, 1955b) have remarked on the association of the pinfish with beds of aquatic vegetation, and they have explained the relative scarcity of the species from the Gulf beaches of northern and southern Texas on the basis of sparsity or absence of aquatic vegetation in the area. The same association undoubtedly holds true in southeastern Louisiana since, as mentioned earlier, the vegetation is of significance directly as food for the adults, and indirectly as a source of small invertebrates which are consumed by both the young and adults. The distribution of their food items in Lake Pontchartrain suggests further that whereas adult pinfish must browse among the vegetation of the limited grassy shallows, the young probably feed on the bottom in much the same habitat.

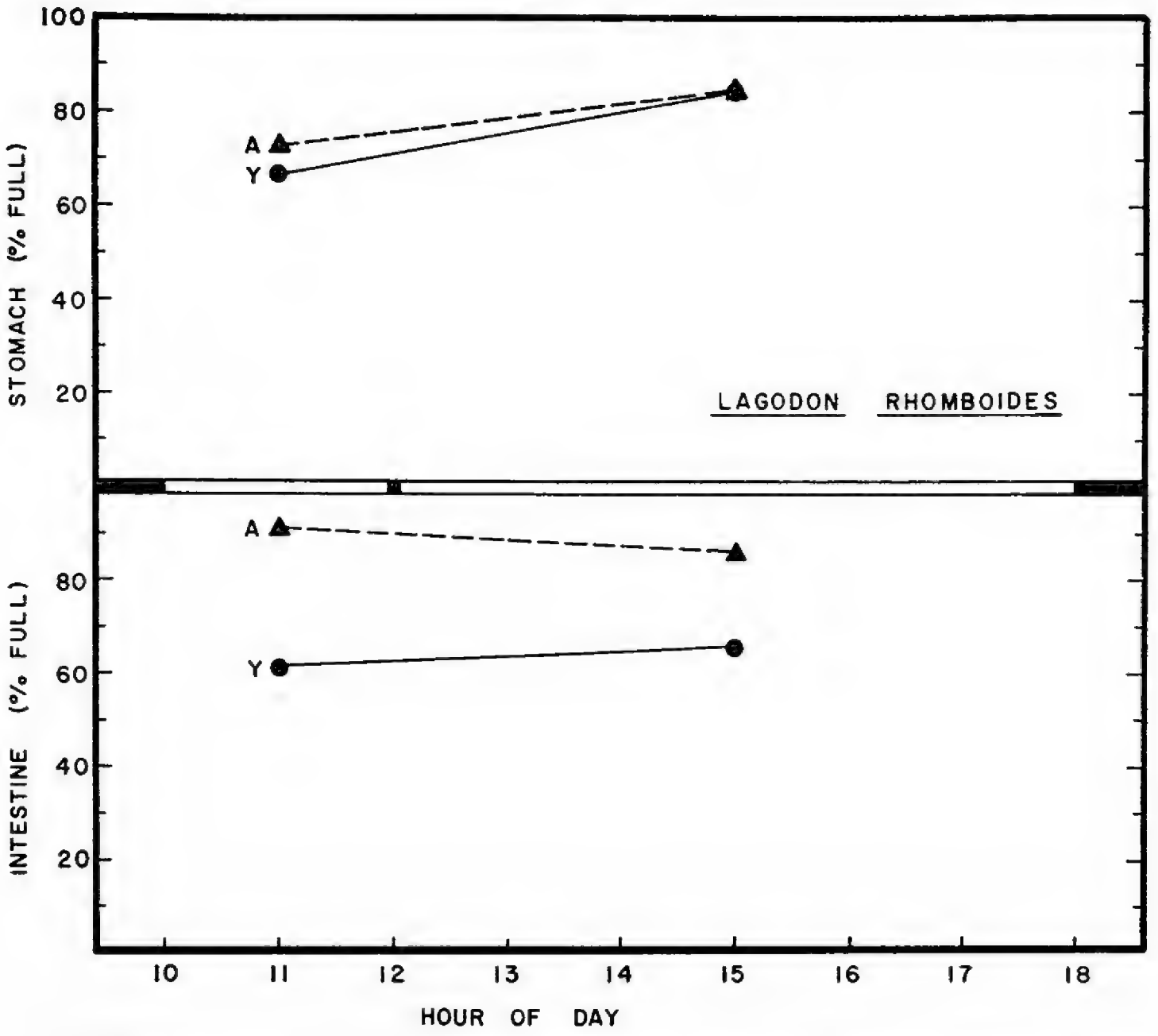

FIG. 15. Hourly pattern of percent-fullness of stomach and intestine of *Lagodon rhomboides* (young and adult).

Like its relative, the sheepshead, the pinfish exhibits a row of incisor-like teeth which are employed for grazing upon vegetation, picking up small invertebrates, and, perhaps, scraping invertebrate epifauna from solid surfaces. Size differences seem to preclude much overlap in food requirements of the adults of the two species. Competition of adult pinfish with young sheepshead appears to be avoided largely by differences in habitat utilization.

BOTHIDAE

Paralichthys lethostigma Jordan and Gilbert. Southern Flounder

Gunter (1945) reported the examination of 16 large flounders (240–490 mm.) from southern Texas, eight of which contained food. Seven had consumed fishes including mullet, anchovies (*Anchoa mitchilli diaphana*), pinfish (*Lagodon rhomboides*), mojarra, and other unidentified species. In addition, three flounders contained penaeid shrimp (*P. aztecus* and *P. setiferus*) and a stone crab. McLane (1948) mentioned that in the St. Johns River of Florida, the southern flounder consumes large numbers of the locally abundant shad, *Signalosa petenensis vanhyningi*. Knapp (1949) examined 24 specimens from Texas and found that fishes, including the menhaden, were present in over 40 percent of the stomachs, shrimp were present in 50

percent, and miscellaneous invertebrates occurred in less than five percent. In northern Texas, Reid (1955b) examined the stomachs of seven specimens (159–265 mm.) and found fish in three of the stomachs while shrimp occurred only once.

A total of 19 specimens (113–380 mm.) from Lake Pontchartrain were examined, of which only 14 contained recognizable food. Fishes constituted 89 percent of the total food volume and included anchovies (*Anchoa mitchilli diaphana*) (41 percent), small croakers, (*Micropogon undulatus*) (2 percent), and a large quantity of unidentifiable fish remains (46 percent). Crabs made up about seven percent of the food and included *Callinectes sapidus* as well as *Rithropanopeus harrisii*. Schizopods, clams (*Rangia cuneata*), small gastropods, and undetermined organic material made up less than two percent each.

The above studies indicate that adult southern flounders are highly predaceous consuming large quantities of small fishes and smaller amounts of crabs and shrimp, which they apparently attack either upon or near the bottom. The relative percentages of fishes and shrimp utilized, however, appears to vary from one environment to another and may be related to availability. Young flounders probably prey upon small bottom invertebrates.

Soleidae

Trinectes maculatus fasciatus (Lacépède). Hogchoker

Hildebrand and Schroeder (1928) examined the stomachs of 17 hogchokers from Chesapeake Bay and concluded that the species feeds primarily upon annelids supplemented by occasional small crustaceans and strands of algae. Reid (1954) mentioned that all stomachs which he inspected were devoid of food, although they usually contained quantities of sand.

Ten hogchokers (61–74 mm.) from Lake Pontchartrain were examined, but the stomachs of only three contained recognizable food. Amphipods of the genus *Corophium* were present in all three stomachs and made up about 50 percent of the contents. Undetermined organic matter and detritus comprised the remainder. Examination of the intestinal contents revealed that the hogchokers had also consumed other microcrustaceans, dipteran (chironomid) larvae, foraminifera, and seeds. Although quite meager, the above data suggest that the hogchoker subsists largely upon a diet of small bottom-living invertebrates supplemented by quantities of organic detritus and other materials which it gleans from the surface of the bottom.

Invertebrates

Mactridae

Rangia cuneata Gray. Common Rangia, Clam

Three specimens of the common rangia (35–38 mm.) from Lake Pontchartrain were examined, and all of the stomachs contained food. Unidentifiable detritus made up about 70 percent of this material, and sand constituted 10 percent. Enormous numbers of small, regular, round bodies were observed in two of the clams, and these made up an estimated 17 percent of the total food volume. These bodies, which were barely distinguishable at 1000x magnification, were assumed to be minute protozoans or individual cells derived from disintegrated colonies of blue green algae (*Anabaena*

spp. or *Microcystis* spp.). Additional material present in trace amounts included eggs (or cysts), a variety of bottom diatoms, foraminifera, and bits of vascular plant material.

In Lake Pontchartrain the common rangia is most abundant on the muddiest bottoms in waters of maximum turbidity. As indicated by the above analyses and by observations in laboratory aquaria, the species is a typical "filter feeder", and in view of the high percentage of detritus ingested a simple straining action with very little selectivity is suggested.

Penaeus setiferus (Linnaeus). White Shrimp

Williams (1955) reported on stomach analyses of 184 young and adult penaeid shrimp from the estuaries of North Carolina. He found that the stomachs were generally filled in the summer and fall, but were nearly always empty in winter. Williams listed the most abundant food materials as follows (in order of decreasing frequency of occurrence), unrecognizable debris (probably a mixture of digesting tissue and organic deposit from the bottom), chitin fragments (from crustaceans), setae (probably from annelids), worm jaws (annelid), plant fragments, and sand. Other materials occurring in smaller quantities included foraminifera, minute gastropods and lamellibranch shells, squid suckers, complete small fishes, fish parts (scales, muscle fibers, remains of gut, mandible, ribs, eye lens), eggs, seed pods, and other materials. Williams emphasized that most of the remains which he encountered were either large or very hard, in either case, materials which would not readily pass through the straining apparatus of the pyloric stomach. Since such materials might accumulate over a period of time, he suggested that unrecognized, softer, more digestable matter could easily form the bulk of the shrimp diet.

Flint (1956) studied the food of penaeid shrimp from Grande Isle, Louisiana and Biloxi, Mississippi (localities verified by personal correspondence). Small shrimp (*ca.* 10 mm.) contained chiefly cropped filaments of blue green algae and such diatoms as ordinarily would have been found adherent to them in the natural habitat. Adult shrimp, however, were found to have consumed large quantities of bryozoans, some algae, and a few small pieces of sponge and coral. The algae included primarily lithophytic diatoms which may have been taken in incidentally, adherent to other materials. A few fragments of roots and stems of vascular plants and bits of sawdust also were encountered. Flint noted that partial or complete digestion of the algal protoplasts had taken place. He concluded that in the turbid coastal waters (of Mississippi and Louisiana), blue green algae which thrive in low light intensities probably serve as a major food for both young and adult shrimp, although the latter consume a diversity of materials among which bryozoans, lithophytic algae, and diatoms appear to be outstanding.

In the present study the stomach contents of ten white shrimp (91–142 mm.) were examined, all of which contained food. Detritus and ground organic matter made up 58 percent of this material. Mollusks, comprising 12 percent included many minute clames *(Rangia cuneata)* and a few small gastropods. Microcrustacea made up less than four percent of the stomach contents and included ostracods and harpacticoid copepods. Insect remains were evidenced by traces of dipteran and coleopteran larvae. Numbers of foraminiferans were present in six of the stomachs, and traces of vascular

plants were noted twice. In addition to the above materials, all shrimp contained quantities of sand.

Pearson (1939) successfully reared post-larval white shrimp (5–35 mm.) in laboratory aquaria. He found that green algae were consumed in quantity, but alone this material seemed insufficient to satisfy the hunger of the young shrimp. When placed in aquaria containing a shallow layer of estuarine bottom deposits of sand and organic debris, however, the young shrimp fed well and thrived on this material. At a length of about 15 mm. other food was introduced such as raw fish, angleworms, and shrimp meal which also were taken readily as food. More recently, Johnson and Fielding (1956) reported success in rearing adult white shrimp on a diet of fish meal and also upon fresh fish. In special growth experiments shrimp were found to consume as much as 10 percent of their body weight of fresh fish per day.

The accumulated evidence suggests that, whereas both young and adult white shrimp are omnivorous, they feed largely upon organic detritus of the estuarine bottom. This substance is supplemented with more concentrated food material of animal and vegetable origins, both fresh and decaying, from a great variety of immediate sources. In Lake Pontchartrain large concentrations of white shrimp were sometimes observed feeding in shallow mud flats on hot summer days, especially in the rich deltaic deposit areas of tidal streams which drain the north shore marshes. Much feeding must also take place in deeper waters since shrimp captured a mile or more from shore generally exhibited full stomachs.

Palaemonidae

Macrobrachium ohione (Smith). River Shrimp

Ten specimens of the river shrimp (48–81 mm.) from Lake Pontchartrain were examined, and all contained food material. Finely-ground detritus and bits of organic material made up over one-half of the diet, and sand constituted almost 20 percent of the stomach contents. Of the remaining identifiable material, clams *(Rangia cuneata)* made up the highest percentage. These were frequently broken, although the stomach of one river shrimp contained a total of 33, mostly unbroken clams, the largest of which measured 1.5 mm. Miscellaneous items included ostracods, bits of arthropod integument, minute gastropods, hydroid "stems", sponge spicules, tintinnids, foraminiferans, filamentous algae (*Cladophora* sp.), diatoms (species of *Cymbella, Navicula,* and *Pinnularia*), eggs and cysts, and remains of vascular plants. Three of the river shrimp contained fish remains including eye lenses, vertebrae, ribs, otoliths, scales, and macerated fibers which appeared to be muscle tissue. Several individuals contained quantities of minute round bodies similar to those encountered in stomachs of *Rangia cuneata* (mentioned earlier).

These analyses indicate that the river shrimp is a general bottom scavenger feeding upon bits of animal and vegetable material which it sifts from the bottom surface material. The bottom detritus itself forms a significant portion, if not the bulk, of the diet of this species. The nature of the stomach contents further suggests that the river shrimp and the white shrimp were for the most part feeding on different types of bottoms.

Portunidae

Callinectes sapidus Rathbun. Blue Crab

In his discussion of the life history of the blue crab, Hay (1904) considered the food and the feeding habits of the species. He noted that in shallow back-waters the

blue crab often stalks and consumes small fishes and that occasionally it nibbles at tender shoots of eel grass and other aquatic vegetation. He considered the "favorite" food of the blue crab, however, to be decaying flesh and other putrid matter and noted that large numbers of crabs were attracted to the offal from stables and water closets overhanging the water. Hay also indicated that injured crabs, small crabs, and soft crabs are sometimes eaten by stronger individuals, and he concluded that while the blue crab consumes a variety of foods, it is preeminantly a scavenger and a cannibal.

In the Lake Pontchartrain study a great variety of materials was encountered in the stomachs of all sizes of crabs, although food differences between young and adults were not pronounced (Table 13 and Fig. 16). Crustacean remains constituted the most abundant material in the stomachs of small individuals, making up over one-third of the food in the 30–74 mm. group. This material decreased to 10 percent of the food volume in the largest individuals. Included in this material were the remains of both the blue crab (*Callinectes sapidus*) and the mud crab (*Rithropanopeus* harrisii), as well as unidentified pieces of crustacean exoskeletons. Greatest utilization of the mud crabs occurred in the 75–124 mm. class where they made up 16 percent of the food volume, and small blue crabs achieved a maximum of 13 percent in

TABLE 13

Occurrence of food items in stomachs of 124 *Callinectes sapidus*

	30.0–74.0 mm. 29 examined 24 with food		75.0–124.0 mm. 31 examined 27 with food		125.0–147.0 mm. 24 examined 23 with food		148.0–197.0 mm. 40 examined 29 with food	
FOOD ITEMS	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume	Percentage of tracts* containing item	Percentage of total stomach volume
Crabs (undet.)	13.8	2.7	12.9	4.9	16.7	5.7	12.5	4.3
Rithropanopeus harrisii	.....	.....	16.1	15.6	4.2	0.2	5.0	0.1
Callinectes sapidus	10.3	1.4	3.2	2.5	8.3	13.0	7.5	5.0
Cirripedia	.....	.....	6.5	0.1	....	.....	.....	.....
Crustacea (undet.)	31.0	31.7	9.7	2.0	20.1	3.5	10.0	1.0
Odonata	.....	.....	3.2	0.2	4.2	0.2	.....	.....
Annelida	.....	.....	6.5	0.1	4.2	T	.....	.....
Mollusca								
Rangia cuneata	41.4	32.4	45.2	20.2	70.8	30.0	57.5	46.5
Mytilopsis leucopheata	....	.....	6.5	0.3	25.0	19.4	20.0	11.9
Gastropoda	13.8	1.9	12.9	9.0	29.2	5.5	25.0	5.0
Hydroids	3.4	0.3	6.5	0.2	8.3	0.5	2.5	T
Vertebrata								
Fish remains	3.4	0.5	6.5	0.4	16.7	1.6	17.5	5.4
Bottom Diatoms	.....	.....	3.2	0.1	.....	.....	.....	.....
Algae—filamentous	.....	.....	12.9	3.0	4.2	T	2.5	0.3
Vascular plants	6.9	0.4	25.8	8.1	20.8	0.8	10.0	2.0
Organic mat. (undet.)	17.2	7.7	35.5	13.9	25.0	5.9	17.5	8.8
Detritus	37.9	12.1	32.3	12.8	33.3	12.7	15.0	9.7
Sand	37.9	9.1	41.9	6.4	29.2	1.7	2.5	T

SUMMARY

Crabs, Undet. Crusts	35.8	25.0	22.4	10.4
Mollusks	34.3	29.5	54.9	63.4
Fish remains	0.5	0.4	1.6	5.4
Vegetation, misc.	0.7	11.8	1.5	2.3
Detritus, undet.	19.8	26.7	18.6	18.5
Sand	9.1	6.4	1.7	T

* Stomach only.

the diet of the 125–147 mm. size group. Following a molt the blue crab may consume its own shed exoskeleton, and it is likely that much of the blue crab shell encountered in the stomachs was simply obtained in this manner. The evidence here indicates that some cannibalism does occur, however, since fresh muscle fibers were frequently found still attached to the consumed shell fragments. *Callinectes sapidus* is known to be cannibalistic when confined in "holding" pens, especially if hard and soft individuals are confined together (Benedict, 1940; Cargo and Cronin, 1951), and the present work bears out the suggestion of Hay (*op. cit.*) that cannibalism is also of widespread occurrence in the natural population.

Mollusks also appeared as an important elment in the diet of the blue crabs, constituting one-third of the food of the smallest individuals and increasing to almost two-thirds of the food volume of the largest size class. These mollusks included small clams *(Rangia cuneata)*, mussels *(Congeria leucopheata)*, and gastropods *(Melampus coffeus* and *Neritins virginico*, both of which are inhabitants of the marginal *pus coffeus* and *Neritina virginica*, both of which are inhabitants of the marginal

Fish remains were not significant in the diet of the smaller size groups, and even in the largest blue crabs they made up only 5 percent of the food. Vegetation was

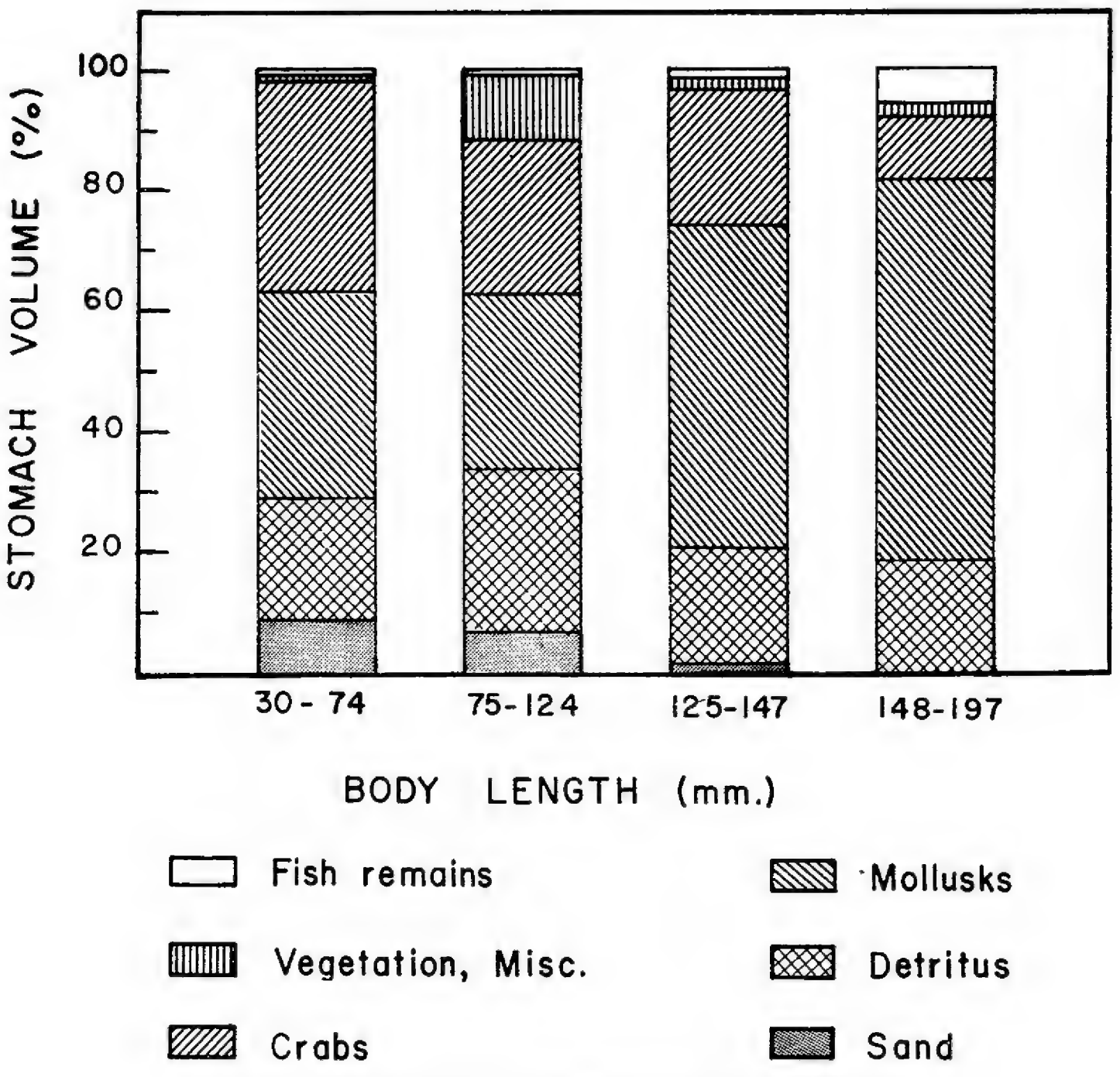

Fig. 16. Ontogenetic food progression of *Callinectes sapidus*.

seldom encountered except in the 75–124 mm. group where it made up 11 percent of the consumed material. Detritus and undetermined organic material, however, were of considerable importance throughout the size range investigated, constituting from one-sixth to one-fourth of the stomach contents within each size class. Sand made up nine percent of the contents of the smallest size group and declined thereafter to less than one percent.

As indicated for the white shrimp, small or easily-digested soft tissues may comprise a larger percentage of the food of the blue crab than is evident from routine stomach analyses. The general types of food seem clear, however, even if quantitative aspects may be somewhat distorted. As a detritivore, this crab consumes large quantities of bottom debris and decomposing organic matter. As a bottom predator, it takes in numbers of small crabs (including its own kind), clams, mussels, and snails, as well as occasional aquatic insects, barnacles, and probably other small invertebrates and fishes. As a general scavenger, this species is attracted to decaying flesh in baited nets and traps, and undoubtedly the blue crab consumes large quantities of decaying fishes and other animals under natural conditions. Benedict (1940) mentioned that blue crabs are attracted to nets and lines baited with the flesh of many species of fishes. Cargo and Cronin (1951) listed fish as the main item in the diet of the blue crabs in Chesapeake Bay, adding that the species also takes in a wide variety of animal and plant matter including seaweeds and marsh plants. In Lake Pontchartrain this species is a detritivore, bottom predator, and general scavenger; any less complete designation would seem inadequate.

The stomachs of young blue crabs tend to be most full in the morning hours, and it appears that most of their feeding takes place either at night or during the early morning with less feeding activity in the afternoon (Fig. 17). Adults, on the other hand, exhibit the fullest stomachs in the middle of the afternoon, indicating that they are primarily daytime feeders. The significance of this difference in feeding time is not clear. It might be supposed that the young, living in shallowest waters, are faced with the necessity of avoiding extreme temperatures or excessive predation during the daylight hours, and that the adults feeding chiefly in deeper more turbid waters, are less limited by these factors. In partial substantiation of this idea, Lambou (1952) recorded the presence of immense numbers of crabs of all sizes in the shallow, brackish-water lagoons north of Lake Pontchartrain, and he indicated that the small crabs were especially abundant at night when the shallow water appears to be alive with them. In view of information presented elsewhere in this paper, selective factors due to predation pressure on this species must be enormous.

Discussion

Ignoring details, the food studies reveal two primary food chains within Lake Pontchartrain. The first pathway proceeds from copepods (*Acartia*) through small fishes (*Anchoa, Brevoortia,* very young sciaenids, etc.), to larger predators. The second proceeds from small benthic invertebrates through larger invertebrates and small bottom-dwelling fishes (catfishes, young sciaenids, etc.), to the same large predators. Organic detritus, which was prominent in the food of the fishes and larger invertebrates, probably also serves as an important source of nutrition for the cope-

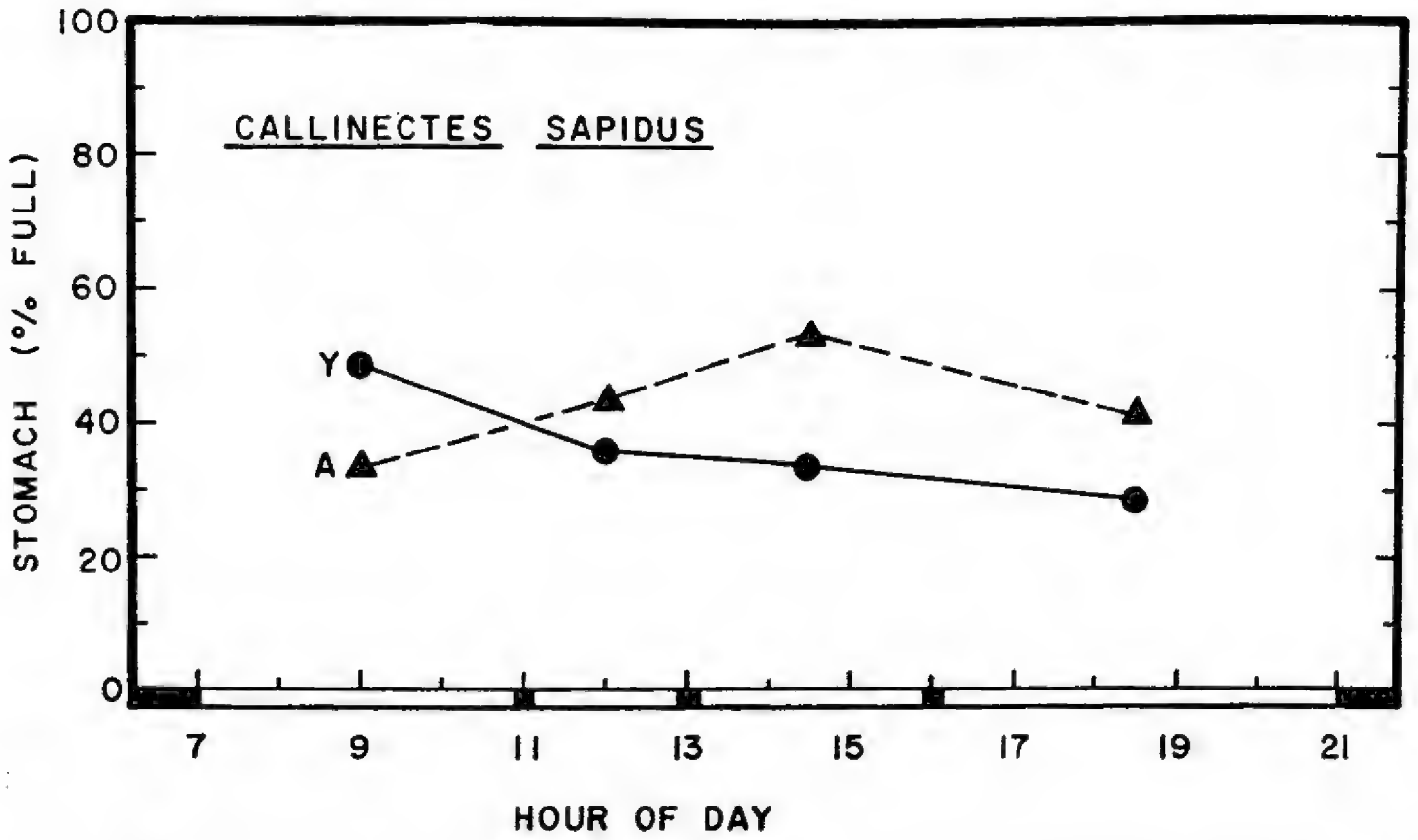

FIG. 17. Hourly pattern of percent-fullness of stomach and intestine of *Callinectes sapidus* (young and adult).

pods and small benthic invertebrates of this turbid estuary. Such detritus has a very complex origin (cf. Gneri and Angelescu, 1951), and it has been shown by other workers to be rich in bacteria (Baier, 1935; ZoBell and Feltham, 1938, 1942; Burkholder and Bornside, 1957).

An ontogenetic progression of food stages was clearly demonstrated for several of the well studied species, and for one species (Atlantic croaker) as many as four distinct nutritional stages were recognized. Within a given stage considerable substitution of food items was often observed. In some cases it was possible to correlate ontogenetic changes in food utilization with changes in morphology, habitat, feeding time, and behavior. As a result of their highly varied diets including much detritus, most, if not all, of the species examined are considered to be omnivorous. Distinct trophic levels (in the sense of Lindeman) were not recognizable in this estuarine community.

Summary

The physical environment of Lake Pontchartrain was found to be characterized by moderate temperature, generally low salinity, and very high turbidity, although considerable variations in these factors were noted. Food studies, including 1,399 quantitative and about 100 qualitative stomach analyses, were carried out on thirty-five of the most important species comprising the estuarine community. These included the following: bull shark, longnose gar, spotted gar, alligator gar, bigeye herring, gulf menhaden, gizzard shad, threadfin shad, southern bay anchovy, gaff-topsail catfish, sea catfish, blue catfish, channel catfish, Atlantic needlefish, striped mullet, silverside, yellow bass, largemouth bass, common jack, freshwater drum, silver perch, sand squeteague, spotted squeteague, spot, Atlantic croaker, black drum, red drum, gulf sheepshead, pinfish, southern flounder, hogchoker, common rangia (clam), white shrimp, river shrimp, and blue crab.

A definite ontogenetic progression of food stages was recognizable in many species, and most were considered to be omnivorous. Organic detritus was prominent in the diet of most species. Two partial food chains (planktonic and benthonic) were found to support the top predators, but distinct "trophic levels" among the consumers were not recognizable.

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Systematics and Zoogeography of the Clinid Fishes of the Subtribe Labrisomini Hubbs[1]

VICTOR G. SPRINGER[2]

Department of Zoology and Institute of Marine Science
The University of Texas
Port Aransas

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[2] Present address: State Board of Conservation Marine Laboratory, Maritime Base, Bayboro Harbor, St. Petersburg, Florida.

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Introduction

The subtribe Labrisomini Hubbs, 1952, is comprised of the genera *Labrisomus* and *Malacoctenus*. These two genera contain the most recognized species and are the most widely distributed of the fishes of the family Clinidae. They are, in addition to this, two of the most common genera found inhabiting the shallow waters of the rocky coastlines and coral reefs of the American tropical regions, although not restricted to these areas. Despite and because of this commonness, many of the forms have remained undescribed; many have been described under numerous synonyms; and many have been misidentified in the literature and museum collections. Until recently (Hubbs, 1953), neither of these genera had been subjected to a critical revision, although Longley (in Longley and Hildebrand, 1941) apparently was considering a revision of the Atlantic forms at the time of his death. This gap in ichthyological knowledge is all the more magnified when one considers that because of the sedentary nature of these forms, a knowledge of them would contribute significantly to the delimiting and understanding of the zoogeography of the regions they occupy. Other members of the Clinidae, especially *Paraclinus* (Hubbs, 1952; Springer, 1955a) and *Gibbonsia* (Hubbs, 1952), have already been demonstrated as signposts of zoogeographic consequence.

The present study has been undertaken for the purpose of clarifying the somewhat involved systematics of the group, and the exposition of their zoogeographic importance in the regions they occupy.

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Methods

Measurements were made with a pair of finely sharpened dividers and estimated to the nearest tenth millimeter on a ruler graduated in half-millimeters, or divided into other body parts. Measurements of body parts are recorded as per cent of the standard length.

STANDARD LENGTH was measured from the median anterior tip of the upper lip, with the mouth in normal closed position (*i.e.* the upper jaw not protracted) to a point on the midlateral posterior margin of the hypural vertebra. LENGTH is always standard length. HEAD LENGTH, SNOUT LENGTH, and MAXILLARY LENGTH were measured from the same anterior point as the standard length. Head length was measured to the most posterior membranous margin of the opercle, but not including the attached branchiostegal membrane; snout length was measured to the nearest point on the anterior bony orbital margin; and maxillary length to the most posterior point of extension of the maxillary bone. BONY ORBITAL DIAMETER is the greatest horizontal bony orbital diameter. DORSAL SPINES were measured by pressing one point of the dividers in the posterior angle formed by the spine and the dorsal body contour, and extending the other point to the tip of the spine; any curvature of the spines was ignored. SHORTEST PELVIC RAY LENGTH was measured from the base of the ray to its tip with the ray in a straight position. This measurement was divided into the longest ray using the level of the tip of the shortest ray as the first point of reference on the longest ray. The INTERSPACE (Fig. 1) between the nuchal cirri bases was measured as the distance between the two most median points of attachment of the cirri bases, excluding the medianly overlapping edges of the laminae supporting the cirri. This measurement was then divided into a single cirri base.

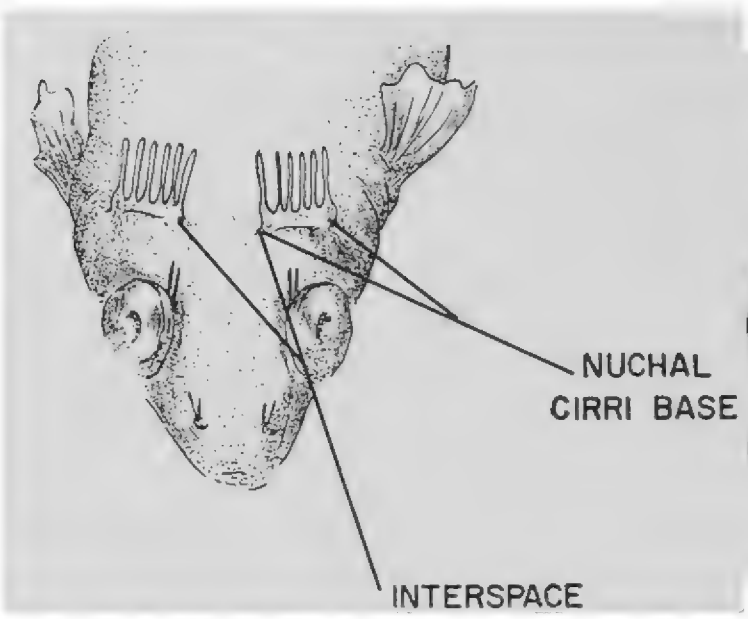

FIG. 1. Position of Interspace between Nuchal Cirri Bases.

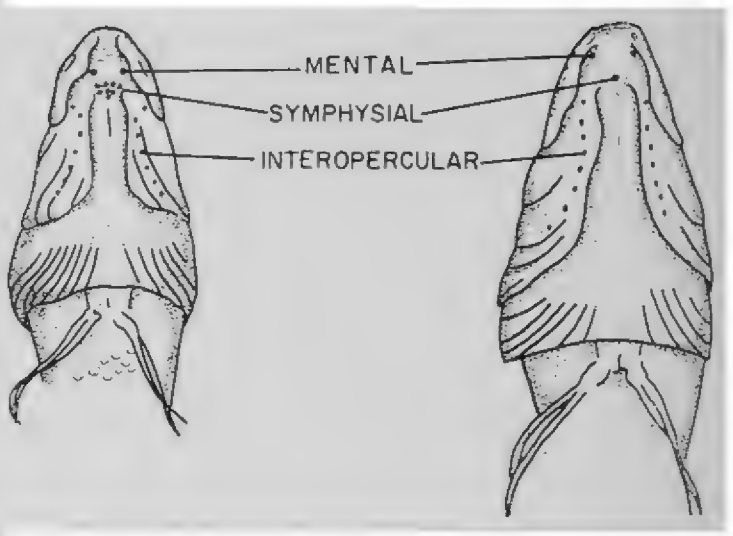

FIG. 2. Disposition and Nomenclature of Mucous Pores on the Ventral Side of the Head in Labrisominids.

The last two DORSAL and ANAL FIN RAYS were counted separately and not recorded as one as was done by Hubbs (1952, 1953). Dorsal fin elements are reported as formulae actually found; hence, if dorsal counts of XIX.19; XIX,20; XIX,21; and XX,19 were made, they are reported as XIX,19 to 21 or XX,19 (instead of XIX or XX,19 to 21, which can be misinterpreted to indicate counts of XX,20 or XX,21). All of the PECTORAL rays and all segmented CAUDAL rays were counted. For the latter, an almost undeviating count of 13 is obtained; this technique obviates subjective discussions as to how to count reduced rays at the dorsal and ventral caudal margins. LATERAL LINE SCALES were counted as all scales in the series whether bearing mucous tubes or not. The last scale of the series on fishes which have scales with tubes on the caudal fin, is the last scale with a tube. When the lateral line was incomplete, the most posterior scale originating lateral to the hypural vertebra was the last scale counted. Scales above the anterior lateral line were counted as the number of scales touched by a vertical line passing from the lateral line to the base of the fifth dorsal spine. GILL RAKERS were counted as total elements, including rudiments, on the first gill arch. SYMPHYSIAL PORES (Fig. 2) were counted while directing a stream of air in the symphysial region. All pores posterior to the two mental pores (just posterior to the ventral lip folds), medial and anterior to the series of interopercular pores, and anterior to the fold of the fused branchiostegal membranes, were counted.

The BREAST was considered to be that portion of the ventral area of a specimen posterior to a line across the posterior margin of the bases of the pelvic fins and anterior to a line extending across the body between the distal margins of the fleshy bases of the pectoral fins. The VENTER extends from the posterior margin of the breast posteriorly to the anus.

Counts and measurements appearing in parentheses are modes.

As is often true when very large series of specimens are examined, unique specimens come to light. In the present study the very rare exceptions where one or three anal spines were present; one pelvic fin was absent; soft dorsal rays occurred between the spines; or a ctenoid scale appeared in the lateral line, are not reported in the descriptions.

The descriptions are arranged so as to make possible a comparison of the species. These include the characters considered most useful for identification.

The synonymies are an attempt to include all publications containing reference to the

particular taxon concerned. It was not always possible to examine the material discussed in these publications, or to tell with certainty from the discussions to what taxa the names referred. All such citations are marked with an asterisk, and are included in the synonymy of that species most probably correct.

Unless stated otherwise, coloration is described from preserved specimens.

Abbreviations

Below are given the abbreviations used in the lists of material examined. All UCLA numbers are collection numbers and not specimen or lot numbers.

AMNH—American Museum of Natural History, New York; ANSP—Academy of Natural Sciences of Philadelphia; BMNH—British Museum (Natural History), London; CAS—California Academy of Sciences, San Francisco; CNHM—Chicago Natural History Museum, Chicago; IMSC—Institute of Marine Science Collections, Port Aransas, Texas (specimens do not bear numbers); MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; NYZS—New York Zoological Society, New York; SU—Standford University Natural History Museum, Stanford, California; TNHC—Texas Natural History Collection, University of Texas, Austin, Texas; UCLA—University of California at Los Angeles; UM—University of Miami Ichthyological Collection, Coral Gables, Florida; UMMZ—University of Michigan, Museum of Zoology, Ann Arbor, Michigan; USNM—United States National Museum, Washington, D.C.; UZMK—Universitetets Zoologiske Museum, Copenhagen.

Systematics

As a result of considerable parallel and/or convergent evolution within the genera *Labrisomus* and *Malacoctenus*, it is difficult to establish mutually exclusive generic limits for any character. The most constant differences are found in the size and dentition of the jaws. Examination of stained preparations of several species of both genera revealed no striking differences.

Some difficulty may be encountered in the generic allocation of specimens of *L. nigricinctus*, but the following key will separate all specimens of *Labrisomus* and *Malacoctenus* that I have examined.

Maxillary length 10.2 to 19.0 percent of standard length (usually more than 13 and rarely less than 12 percent); preorbital barely or not sheathing posterodorsal portion of maxillary when mouth is closed; more than two rows of small teeth always present behind large outer row in at least upper jaw (those in lower jaw frequently obscured by fleshy folds); teeth present or absent on palatines (if absent, scales are always present on upper margin of opercle and pectoral base); one or more scales usually present on upper margin of opercle (they may be deeply imbedded, but if absent, teeth are always present on palatines); interspace between bases of nuchal cirri contained less than three times in a single base; membranes of fins with or without scales ..... *Labrisomus*

Maxillary length 7.9 to 11.2 percent of standard length (usually 8.5 to 9.5 and rarely more than 10.1 percent); preorbital almost completely sheathing entire maxillary when mouth is completely closed; teeth uniserial in each jaw (four or five small teeth behind outer row in each jaw: *M. erdmani;* teeth biserial in each jaw: *M. macropus;* several rows of small teeth behind large outer row

in each jaw: *M. boehlkei*); teeth never present on palatines; scales never present on upper margin of opercle; interspace between bases of nuchal cirri frequently contained more than three times in a single base; membranes of fins never scaled ..... *Malacoctenus*

LABRISOMUS Swainson

Labrisomus Swainson, 1839: 277 (type *Clinus pectinifer* Valenciennes in Cuvier and Valenciennes, 1836, by original designation).

Lepisoma De Kay, 1842: 41 (type *Lepisoma cirrhosum* De Kay by original designation).

Gobioclinus Gill, 1960b: 103 (type *Clinus gobio* Valenciennes in Cuvier and Valenciennes, 1836, a mixture; subsequent designation of lectotype by Longley, in Longley and Hildebrand, 1941).

Labrosomus Gill, 1860b: 105 (substitute spelling for *Labrisomus* Swainson).

Ericteis Jordan, 1904: 543 (type *Ericteis kalisherae* Jordan by original designation).

Odontoclinus Reid, 1935: 164 (type *Odontoclinus dendriticus* Reid by original designation).

Ctenichthys Rivero, 1936: 69 (type *Ctenichthys interrupta* by original designation).

Brockius Hubbs, 1953: 120, a subgenus (type *Labrisomus* (*Brockius*) *striatus* by original designation).

Labrisomus, *Gobioclinus*, and *Brockius* are retained in this study as subgenera. Specialization is considered to have progressed in the same direction as the sequence of these names. Within each of these subgenera the relationships are not always clear. *Labrisomus philippii* is considered the most primitive member of the genus based upon its large size, high lateral line and pectoral counts, and increased dentition. Specialization within the genus *Labrisomus* is considered to have progressed in the direction of decreased size, dentition, and scalation.

I feel certain that some systematists would relegate each of the above subgenera to the rank of genus, as the differences separating them are trenchant; and if some other systematist revised this group and utilized these names on the generic level, I would find no quarrel with him. The decision for the present usage of these names is based upon similarities and practicality. I believe that the inclusion of all the forms in the genus *Labrisomus* serves to show the close relationships of these forms, while at the same time decreasing the number of names that other workers must utilize. The various phyletic lines are brought out by the use of the subgenus and so the phylogeny of the group is not clouded. Ecologists, physiologists, and others who are usually concerned only with an identifying name, and as few names as possible, will be somewhat relieved. Past usage also makes the comprehensive name *Labrisomus* desirable. All major revisions and geographic studies have incorporated all the forms included here in that genus.

Hubbs (1953) has recently revised the Pacific species of *Labrisomus*. Although these taxa are included in the key below, they are not described in the body of the paper.

Description. Fin rays: dorsal XVII to XXII, 10 to 13; anal II, 16 to 22; caudal 12 or 13 (13); pectorals 13 to 16; pelvics I, 3.

Lateral line 40 to 74; all scales of posterior arc of lateral line with anterior pore exposed (*Brockius*); not more than posterior half of scales of posterior arc of lateral line with anterior pore exposed (*Labrisomus* and *Gobioclinus*). Cheek scaled (*striatus*,

socorroensis, and *philippii*) or naked. Dorsal margin of opercle with or without scales. Fin membranes naked to scaled, except those of pelvics. Prepectoral area and breast completely scaled, except in young.

Jaws with an outer row of large conical teeth, behind which are found two or more irregular rows of smaller teeth. Smaller teeth frequently obscured by fleshy folds (*Labrisomus* and *Gobioclinus*) or clearly represented (*Brockius*). Most posterior of smaller teeth sometimes larger than those anterior (*Gobioclinus*, especially *dendriticus* and *guppyi*) or uniform in size (*Labrisomus* and *Brockius*). Vomerine teeth present. Palatine teeth present (*Gobioclinus* and *Labrisomus*, except *xanti* and *socorroensis*); same size as vomerine teeth or smaller (*Labrisomus*); some noticeably larger than vomerine teeth (*Gobioclinus*); or palatine teeth absent (*Brockius*).

Gill-rakers 8 to 15 on first arch.

Origin of dorsal fin in region above opercle. Length of spinous dorsal base longer than that of soft dorsal. Penultimate dorsal spine about same size as ultimate (*Labrisomus*); smaller than ultimate (*Brockius* and *Gobioclinus*). Soft dorsal higher than spinous portion, except *L. dendriticus* in which the anterior two spines may approach the soft dorsal height.

Anal fin base shorter than dorsal; beginning about midventrally. First anal spine shorter than second, which is shorter than all but last few soft rays.

Second to fourth segmented caudal ray from the bottom the longest; shorter than longest pectoral ray.

Pectoral rays increasing in thickness ventrally; fourth to sixth from the bottom longest.

Pelvic spine visible only by dissection or x-ray. Inner pelvic ray the shortest, contained slightly more than 1 to 3½ times in middle ray, which is the longest.

Cirri present on tube of anterior nostril, above eye, and on nape, increasing in number with age. Interspace between nuchal cirri bases contained less than three times in a nuchal cirri base.

Maxillary length 10.2 to 19.0 percent of standard length (usually more than 13 and rarely less than 12 percent). Posterodorsal portion of maxillary rarely sheathed by preorbital.

Anterior margin of cleithrum never with a hook dorsally.

Sexual dimorphism. Males have a papilla just posterior to the anus containing a common opening for the urinogenital system. Females have an enlarged gential aperture posterior to the anus and a fleshy rugose knob posterior to the genital aperture containing several small papillae, one of which contains an opening from the kidneys. This latter opening is extremely difficult to find, except in large specimens. External genitalia in young of both sexes are similar and malelike.

Secondary sexual dimorphism is exhibited in most species by a larger average size for the upper jaw in males and by increased pigmentation of the females. This pigmentation usually takes the form of heavy spotting and barring on the body and fins, and in *L. nuchipinnis*, a highly reticulate pattern is sometimes formed, especially on the head. In contrast, the males are usually quite uniform in color. Young specimens of both sexes are typically like the female in color, with the pattern changing gradually in males as they approach maturity.

KEY TO THE SPECIES OF LABRISOMUS[3]

A. Palatine teeth present, several of which are considerably larger than those on vomer ..... *Gobioclinus* B

AA. Palatine teeth, when present, same size as, or smaller than those on vomer ..... J

B. Lateral line scales more than 57 ..... (Pacific) *L. (Gobioclinus) dendriticus*

BB. Lateral line scales fewer than 55 ..... (Atlantic) C

C. Length of shortest pelvic ray contained more than 2 times in longest; pectoral rays usually 14 ..... *L. (Gobioclinus) haitiensis* (p. 429)

CC. Length of shortest pelvic ray contained less than 2 times in longest; pectoral rays usually 13 ..... D

D. Peritoneum uniformly dusky gray to black; dorsal spines usually 20; anal rays usually 20; lateral line scales 45 to 48; first dorsal spine longer than fifth ..... *L. (Gobioclinus) bucciferus* (p. 430)

DD. Peritoneum white with scattered large chromatophores; dorsal spines usually 19; anal rays usually 19; lateral line scales 48 to 53; first dorsal spine shorter than fifth ..... E (specimens over 40 mm.)
..... G (specimens 28 to 40 mm.)

E. Symphysial pores always 2 ..... *L. (Gobioclinus) kalisherae* (p. 434)

EE. Symphysial pores more than 2 ..... F

F. A well-developed opercular ocellus present in all specimens; largest specimen, of 100 examined, 88 mm. ..... *L. (Gobioclinus) guppyi* (p. 433)

FF. An opercular ocellus never present; largest specimen, of 216 examined, 49.2 mm. ..... *L. (Gobioclinus) gobio* (p. 436)

G. An opercular ocellus not present ..... H

GG. An opercular ocellus present I

H. Penultimate dorsal spine rarely more than 8 percent of standard length; anal and pectoral fins never heavily spotted ..... *L. (Gobioclinus) gobio* (p. 436)

HH. Penultimate dorsal spine rarely less than 8 percent of standard length; anal and pectoral fins often heavily spotted ..... *L. (Gobioclinus) kalisherae* (p. 434)

I. Gill-rakers 12 to 15, rarely less than 13 ..... *L. (Gobioclinus) guppyi* (p. 433)

II. Gill-rakers 10 to 13, rarely more than 12 ..... *L. (Gobioclinus) kalisherae* (p. 434)

J. Scales fewer than 45; all scales on posterior segment of lateral line with anterior pore of canal exposed ..... *Brockius* K

JJ. Scales more than 55; at least half of scales on posterior segment of lateral line with anterior pore of canal covered by scale to the anterior ..... *Labrisomus* M

K. Scales present on cheek anterior to those at dorsal margin of opercle; length of shortest pelvic ray contained less than 1 4/5 times in longest .....
..... (Pacific) *L. (Brockius) striatus*

KK. No scales present on cheek anterior to those at dorsal margin of opercle; length of shortest pelvic ray contained 1 4/5 to 2½ times in longest ..... (Atlantic) L

L. A well-developed, black ocellus on opercle of all specimens 12 mm. or longer in standard length; body coloration uniformly white with unmarked fins (males) or body with about nine distinct, dark bands extending onto fins (females and young); gill-rakers 9 to 12 ..... *L. (Brockius) nigricinctus* (p. 438)

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[3] Pinto (1957. Bol. Mus. nac. Rio de J. 163: 1–15) has described a new species of Labrisomus *(L. trindadensis)* from Trindade Is. off Brazil.

LL. No black ocellus on opercle; body coloration uniformly dark with indistinct indications of bands on body; fins dark and or spotted; gill-rakers 13 or 14 ..... *L.* (*Brockius*) *albigenys* (p. 437)

M. A distinct black spot or ocellus present on opercle; palatine teeth present ..... (Atlantic) *L.* (*Labrisomus*) *nuchipinnis* (p. 425)

MM. No black spot or ocellus present on opercle; palatine teeth present or absent ..... (Pacific) N

N. Palatine teeth absent ..... O

NN. Palatine teeth present ..... P

O. Many scales on cheek and along entire dorsal part of opercle ..... *L.* (*Labrisomus*) *socorroensis*[4]

——

..... *L.* (*Labrisomus*) *xanti*

P. First dorsal spine longer than opercle depth[5]; most conspicuous color marking a

——

dark humeral spot ..... *L.* (*Labrisomus*) *wigginsi*[6]

——

PP. First dorsal spine shorter than opercle depth; no humeral spot present ..... Q

Q. Fewer than 63 scales in lateral line; caudal peduncle depth more than 9.1 percent of standard length ..... *L.* (*Labrisomus*) *jenkinsi*

QQ. More than 63 scales in lateral line; caudal peduncle depth less than 9.1 percent of standard length (except in *L. philippii*) ..... R

R. Pectoral rays usually 15 or 16; dorsal spines usually 19 or 20; lateral line scales 70 to 74 (rarely 68 or 69); branch or preopercle canal extends less than one-half distance across opercle ..... *L.* (*Labrisomus*) *philippii*

RR. Pectoral rays usually 14; dorsal spines usually 17 or 18; lateral line scales 65 to 69; branch of preopercle canal extends at least one-half distance across opercle ..... *L.* (*Labrisomus*) *multiporosus*

LABRISOMUS (*LABRISOMUS*) *NUCHIPINNIS* (Quoy and Gaimard)
(Plate I Fig. 1)

Clinus nuchipinnis Quoy and Gaimard, 1824: 255; Günther, 1861b: 262; Steindachner, 1867: 47; Günther, 1868: 389 (in part); Kner, 1868: 336; Peters, 1877: 248*; Rochebrune, 1882: 116 (misspelled *nuctipinnis*); Jordan and Gilbert, 1882a: 762; Vinciguerra, 1883: 616*; Guimarães, 1884: 21*; Moquard, 1889: 40 (in part); Cockerell, 1892*; Vinciguerra, 1893: 322*; Osorio, 1896: 63*; Perugia, 1896: 19*; Osorio, 1898: 198*; Boulenger, 1905: 188*; Metzelaar, 1919: 154; Roule and Angel, 1930: 104.

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[4] Hubbs (1953) described this species as *L. soccorroensis*, naming it for Socorro Island in the Revilla Gigedo Islands. As such the original spelling must be considered in error and emended to the form in the above key.

OO. Cheeks naked and fewer than 30 scales in patch on upper margin of opercle .....

[5] In his 1953 key, Hubbs used the term "opercle length", a horizontal measurement. By using his original data I have ascertained that he meant "opercle depth", a vertical measurement. This change is necessary if his key is used.

[6] Hubbs placed this species in the subgenus *Odontoclinus*, which I consider the same as *Gobioclinus*. *Labrisomus wigginsi* has the vomerine and palatine teeth of equal size; 14 or more pectoral rays; the villiform teeth behind the large outer row in each jaw of about uniform size; and the penultimate dorsal spine not noticeably shorter than the ultimate. All of these are typical of *Labrisomus* but not of *Gobioclinus*.

Blennius herminier Le Sueur, 1825: 361.

Clinus pectinifer Valenciennes (in Cuvier and Valenciennes), 1836: 374; Guérin-Méneville, 1829–1844 (date uncertain): Plate 38, Figure 2; Schomburgk, 1848: 16*; Castelnau, 1855: 26; Dumeril, 1858: 263*; Müller, 1864: 631; Poey, 1866: 333.

Clinus capillatus Valenciennes (in Cuvier and Valenciennes), 1836: 377; Schomburgk, 1848: 16*; Poey, 1866: 333.

Clinus herminier, Valenciennes (in Cuvier and Valenciennes), 1836: 379; Günther, 1861b: 264 (spelled *herminieri*).

Clinus canariensis Valenciennes, 1839: 60.

Labrisomus pectinifer, Swainson, 1839: 277; Cope, 1871: 472.

Labrisomus capillatus, Swainson, 1839: 277.

Lepisoma cirrhosum De Kay, 1842: 41.

Clinus fasciatus Castelnau, 1855: 26.

Labrosomus pectinifer, Gill, 1860a: 21; Gill, 1860b: 105; Poey, 1861: 381.

Labrosomus fasciatus, Gill, 1860b: 106.

Labrosomus capillatus, Gill, 1860b: 107; Poey, 1861: 381.

Labrosomus herminieri, Gill, 1860b: 108.

Labrosomus nuchipinnis, Poey, 1868: 398; Goode, 1876: 28; Goode, 1877a: 3 (misspelled *Labrosomuc*); Goode, 1877b: 291; Goode and Bean, 1883: 236; Jordan, 1887b: 908.

Clinus pedatipennis Rochebrune, 1880: 165; Rochebrune, 1882: 116.

Labrisomus microlepidotus Poey, 1880: 246; Jordan, 1887a: 599; Jordan and Evermann, 1896: 468; Jordan and Evermann, 1898: 2363; Jordan, Evermann, and Clark, 1930: 459.

Labrisomus nuchipinnis, Poey, 1880: 246; Smith, 1885: 553; Jordan, 1887a: 599; Lee, 1889: 669; Jordan and Evermann, 1896: 468; Jordan and Rutter, 1897: 133; Jordan and Gunn, 1898: 346*; Jordan and Evermann, 1898: 2362; Fowler, 1899: 119; Evermann and Marsh, 1900b: 311; Gilbert, 1900: 179 (misspelled *nuchipinnus*); Evermann and Kendall, 1900: 93; Barbour, 1905: 130; Bean, 1905: 319; Bean 1906b: 84; McIndoo, 1906: 488*; Rosen, 1911: 66 (in part); Starks, 1913: 74; Nichols and Murphy, 1914: 266*; Fowler, 1915: 49; Fowler, 1916: 251; Fowler, 1920: 145 (misspelled *nuchipinuis*); Nichols, 1921a: 24; Metzelaar, 1922: 135; Breder, 1925: 157; Breder, 1927: 86*; Meek and Hildebrand, 1928: 936; Fowler, 1928: 467; Beebe and Tee Van, 1928: 231; Breder, 1929: 270; Fowler, 1930: 275; Jordan, Evermann, and Clark, 1930: 459; Nichols, 1930: 377; Fowler, 1931: 403*; Longley, 1932: 300; Beebe and Tee Van, 1933: 226; Beebe and Hollister, 1935: 220*; Fowler, 1936: 1037 (in part); Butsch, 1939; 30*: Fowler, 1940: 794; Schmitt and Schultz, 1940: 9; Longley and Hildebrand, 1941: 249; Herre, 1942: 16; Fowler, 1942a: 178; Fowler, 1942b: 77*; Fowler, 1942c: 12; Fowler, 1944: 141 & 472; Fowler, 1945: 327*; Irvine, 1947: 193; Manter, 1947: 300*; Baughman, 1947: 280; Schultz, 1949: 178; Baughman, 1950: 253; Steinitz, 1950: 342; Fowler, 1951: 31; Fowler, 1952: 105; Fowler, 1953: 70; Hubbs, 1953: 115 & 120; Springer and Bullis, 1956: 97; Erdman, 1957: 321.

Labrisomus herminier, Jordan, 1887a: 599; Jordan and Evermann, 1896: 468; Jordan and Evermann, 1898: 2361; Jordan, Evermann, and Clark, 1930: 459.

Lepisoma nuchipinnis, Jordan and Thompson, 1905: 254 (misspelled *nuchipinne*); Ribeiro, 1915: 9.

Labrisomus lentiginosus Bean, 1906a: 30; Bean, 1906b: 83; Fowler, 1930: 275; Jordan, Evermann, and Clark, 1930: 459; Beebe and Tee Van, 1933: 277.
Labrisomus canariensis, Starks, 1913: 74; Hubbs, 1953: 115 & 120.
Clinus (*Labrisomus*) *nuchipinnis*, Arambourg, 1921: 1244; Cadanet, 1950: 271.
Labrisomus fasciatus, Fowler, 1942a: 178.
Labrisomus bahamensis Fowler, 1947: 8.

Description. Fin rays: dorsal XVII, 12 or 13; XVIII, 10 to 13; XIX, 11 or 12; or XX, 12 (XVIII, 12 in over 90 percent of specimens); anal II, 17 to 19 (18 or 19); pectorals 13 to 15 (14). Lateral line 64 to 69 (65 to 67). Gill-rakers 10 to 13 (11 or 12).

Head usually 28 to 31 percent of standard length in specimens over 35 mm. Bony orbital diameter less than snout length in specimens over 40 mm. First dorsal spine usually less than 9 percent of standard length; rarely longer (usually shorter) than any other dorsal spine in specimens over 70 mm.; never longer than sixth through last dorsal spines. Length of shortest pelvic ray slightly more than 1 to 1½ times in longest. Interspace between nuchal cirri bases contained ⅘ to 2⅔ times in a single base. Maxillary 12.7 to 17.4 percent of standard length. Frequently reaching lengths over 100 mm.; largest specimen examined: 176 mm.

Teeth present on palatines.

Scales on upper margin of opercle, prepectoral area, and venter, varying with geographic distribution and size of specimen. In specimens from Natal, Brazil, scales are present on these portions of the body at less than 35 mm., and are obvious at all sizes. In specimens from Panama, scales are developed in these regions sometime between 29 and 42 mm., and are still apparent in specimens of at least 100 mm. In specimens from Marineland, Florida, scales in these body areas do not develop until sometime between 39 and 56 mm., and in large specimens the opercular patch of scales has usually disappeared. Specimens from Vero Beach, Florida, may or may not have scales in these regions at 38 mm. The disappearance of the opercular patch of scales is also true of large specimens from Bermuda. The largest specimens are known from Florida and Texas.

Adult type color pattern is not recognizable until a length of about 20 mm. is attained. Specimens smaller than 18 mm. may be pelagic (planktonic) and are uniformly light with very few melanophores. Specimens of 19 mm., or less, taken in a plankton net off Bimini, Bahamas, are slender and light, as was a 19.3 mm. specimen from off the coast of Colombia. Of two specimens of this same size from Puerto Rico taken in a rocky area, both are greater in depth than those mentioned above; one had acquired adult type coloration, and the other showed indications of color pattern.

An opercle blotch or ocellus is always present in specimens over 25 mm., and most specimens have a blotch on the anterior two or three dorsal spines; this latter blotch decreases in distinctness with size above 120 mm. Females have a more spotted or reticulate pattern than males, and bars on the body are better exhibited. In any large series of specimens there is considerable variability, and color patterns of the opposite sex may occur in particular specimens. In life, Texas specimens may vary from a dark violet brown to a uniformly light cream with dusky stripes. The following description is based on preserved specimens from Natal, Brazil.

Body with five or six irregular bands, only three or four of which are readily distinguishable. Bars usually mottled (females) or solid (males), extending well onto the dorsal and anal (young) or only faintly so (adults). Area between bars lighter, spotted,

or with a reticulate pattern (females), or uniform (males). Fins, especially the caudal, heavily spotted (females) or usually uniform (males). Opercle with a distinct black ocellus or a diffuse splotch. Anterior dorsal spines with a similar mark. Usually two or more dark lines radiating posteriorly from each eye, with light bars between them.

Of ten African specimens seen, the color pattern in all had deteriorated, but appeared to agree with the above description.

Discussion. Although specimens from the African coast only as far south as the Gold Coast were examined, literature reference (Osorio, 1898) places the southern limit for this species in the eastern Atlantic at Annobon Island off the coast of French Equatorial Africa.

Significant variation among the populations was found only in counts of the anal rays (Table 1). I am unable to explain these differences, but it is interesting to note

TABLE 1

Geographic Distribution of Total Anal Elements in *Labrisomus nuchipinnis*

Number of Anal Elements	19	20	21	Number of Anal Elements	19	20	21
Florida				Barbados	1	30	13
St. Augustine & Marineland	3	43		Grenada		5	4
Daytona Beach		1		Tobago		12	4
New Smyrna	1	2		Trinidad			2
Brevard County		2		Venezuela		3	1
Vero Beach	2	30	2	Colombia		1	1
Ft. Pierce		1		Panama	2	91	39
West Palm Beach			3	Albuquerque Cay		1	
Ft. Lauderdale			1	Old Providence Island		1	1
Tavernier (Keys)		1		Swan Island			1
Spanish Harbor (Keys)		1		Mexico			
Tortugas (Keys)	2	6		Campeche Banks		4	6
				Vera Cruz		2	4
Bahama Islands				Texas			
New Providence (and environs)	13	5		Port Isabel		13	1
Bimini	2	2		Port Aransas		13	
Andros	2						
Abaco	1	1		Brazil			
Turks	3			Isla Fernando Noronha		1	1
Cay Sal Bank	5	1		Natal	2	35	65
				Porto Seguro		2	
Cuba	34	21		Rio de Janeiro		14	
Jamaica	1	2					
Haiti	4	4		Bermuda Islands		42	113
Dominica	1	3					
Puerto Rico	16	11		Eastern Atlantic			
Virgin Islands	13	3		Madeira Islands		3	
St. Martins	4	3		Canary Islands		2	
St. Lucia	4			Cape Verde Islands		1	
St. Vincent	3			Gold Coast		4	

the grouping of the regions on the basis of anal ray counts. Florida, Texas, and the eastern Atlantic fall into one group; the Bahamas, Antilles, and Panama in a second group; and Natal, Brazil, and the Bermudas into a third.

Labrisomus bahamensis Fowler is included in the synonymy of this species for the first time. Fowler's species is based on a very young specimen which has the typical dorsal, anal, pectoral, and lateral line counts of *L. nuchipinnis*.

Relationship. This species is most closely related to *L. multiporosus* (Pacific) from which it differs in the possession of an opercular ocellus and a larger number of gill-rakers on the first arch.

Material. Eight hundred and eighty-eight specimens were examined. One hundred and three from Florida: ANSP 30972, 33007–08, 55908, CNHM 50737, SU 8188, TNHC 3877–84, UM 881, UMMZ 136494, 154825, 158658, USNM 62653, 62628, 88128–29, 91417, 116814, R. W. Harrington (personal collection) H56–24, H55–9C; 63 from the Bahamas: AMNH 7227, 7346, ANSP 74648–53, 74732–33, 72181, 71734 (holotype of *L. bahamensis*), BMNH 1936.6.5.24, UM 57, 58, 537, 882, 1296, University of Miami Marine Lab (no number), USNM 38379; 58 from Cuba: MCZ 12491–98, 12566, 12607, MCZ (no number), UM 56, USNM 4783, 13039, 24780–81, 24948, 24950, 33099, 33104, 33109, 33118, 33127, 33129, 37423, 37426, 37574, 133013, 154868, 37572 (holotype of *L. microlepidotus*); 3 from Jamaica: ANSP 18637, BMNH 97.7.1.3, SU 4967; 8 from Haiti: MCZ 12609–10, USNM 133748; 4 from Dominican Republic: ANSP 16513, MCZ 34695; 29 from Puerto Rico: AMNH 2074, ANSP 12577, 23611, 28852, SU 8247, UMMZ 160623, 171160, 171164, 171208, 171213, 171215, 171220, 171242, 171149, USNM 50197, 63046, 73834, 117438, 126187; 17 from the Virgin Islands: ANSP 74661–62, 10589, BMNH 63.8.7.168–9, USNM 120488, UZMK 12, 45–51, 65, 2; 7 from St. Martins: ANSP 10591–7; 4 from St. Lucia: SU 4257, USNM 42190; 3 from St. Vincent: BMNH (no number), MCZ 26101; 49 from Barbados: ANSP 74464, 74466, 74654–57, SU 32034, USNM 5924; 9 from Grenada: ANSP 52494–99, 52500–02; 16 from Tobago: BMNH 1920.12.174–83, UZMK P76933; 2 from Trinidad: ANSP 74688, BMNH 1902.1.25.10; 4 from Venezuela: USNM 78251–2, 123173–74; 3 from Colombia: USNM 49077, 134905, 163276; 136 from Panama: CNHM 18520–46, 18548–62, SU 17628, 17870, 18605, UCLA W53–268, USNM 81908–16, 148711–12; 1 from Albuquerque Cay: ANSP 74685; 2 from Old Providence Island: ANSP 74684, USNM 107114; 1 from Swan Island: BMNH 1908.7.6.25; 17 from Mexico: CNHM 46654, IMSC (no numbers), USNM 37793; 23 from Texas: TNHC 3885, 4313, 4364, UMMZ 166112; 2 from Isla Fernando Noronha: BMNH 88.1.19.91; 151 from Brazil: AMNH 3809, BMNH 1923.7.30.3.3–4, CNHM 59060, MCZ 4638, 12490, and one skeleton MCZ (no number), SU 22150, USNM 83242, UZMK 4, 6; 159 from Bermuda: AMNH 9031, ANSP 39842–43, 74658–60, BMNH 1872.8.28.54–56, 72.8.28.56, 1880.9.14.23, CNHM 48206, 48271, 48176, MCZ 12489, 32850, 32850A, 34011, 36434, USNM 21240, 21380, 23798, 154753, 164915; 3 from the Madeira Islands: BMNH 99.1.16.17–19; 2 from the Canary Islands: SU 4290; 1 from the Cape Verde Islands: BMNH 64.6.6.52; 4 from the Gold Coast: BMNH 1930.8.26.75, 1932.2.27.21–2, 1939.7.12.34.

LABRISOMUS (GOBIOCLINUS) HAITIENSIS Beebe and Tee Van

(Plate I Fig. 4)

Labrisomus haitiensis Beebe and Tee Van, 1928: 232; Longley and Hildebrand, 1941: 253; Manter, 1947: 300*; Fowler, 1952: 105.

Description. Fin rays: dorsal XX, 10 to 12; XXI or XXII, 10 or 11 (XX or XXI, 10 or 11); anal II, 18 to 22 (20 or 21); pectorals 13 to 15 (14). Lateral line 43 to 46 (many scales lack tubes). Gill-rakers 10 to 13.

Head 29.5 to 31.7 percent of standard length in specimens over 20 mm. Bony orbital diameter considerably greater than snout length in all specimens (orbital diameter always more than 10.5 percent of standard length; snout length always less than 8.6 percent of standard length). First dorsal spine always exceeding 10 percent of standard length; longer than third, fourth, or penultimate dorsal spines. Length of shortest pelvic

ray contained 2½ to 3½ times in longest. Interspace between nuchal cirri bases contained ¼ to ½ times in a single base. Maxillary 12.8 to 15.9 percent of standard length (usually more than 13.5 percent). Largest specimen 58.2 mm.

No differences in color pattern were noted between males and females. All fins of adults are specked or barred. The most distinct barring occurs on the anal fin. There are five or six irregular bands on the body which extend onto the dorsal in diminished intensity (well defined in young up to 30 mm.). The ground color of the body between the bands is light with scattered darker markings. The venter is irregularly dusky, as is the underside of the head. The pectoral fin has a dark crescent mark at the bases of the rays. The color of the head is similar to that of the body. The opercle may or may not have a diffuse blotch on its dorsal portion. There are two dark bars, with a lighter area between, extending posterior to the eye.

Discussion. There is slight variation in total dorsal and anal elements in specimens from different localities. Of eight specimens from Tortugas, Florida, six had thirty-one dorsal elements and one each had thirty and thirty-two. Of nineteen specimens from the northern Bahamas, fifteen had thirty-two dorsal elements, three had thirty-one, and one thirty. Of the specimens from Tortugas, six had twenty-two anal elements and one each had twenty and twenty-one. Of the Bahamas specimens, sixteen had twenty-three anal elements and one each had twenty-one, twenty-two, and twenty-four. Of two specimens from the northwest coast of Florida, one each had thirty-one and thirty-two dorsal elements and both had twenty-three anal elements.

Relationship. This species differs from all other *Gobioclinus* in having typically fourteen pectoral rays and the shortest pelvic ray contained in the longest more than two times.

Material. Thirty-one specimens were examined. The holotype, NYZS 7170, from Port-au-Prince Bay, Haiti; 19 from the northern Bahamas: ANSP 74511, 74662, 74664–6, 74709–11, 74715–6; 8 from Tortugas, Florida: USNM 88121, 116803, and one USNM no number; 1 from a reef thirty miles south of Miami, Florida: USNM 167668; and 2 from off the northwest coast of Florida: USNM 73062 and 129877.

In addition to the above, eight specimens from the Bahamas, USNM 38515, 17 to 18.5 mm., are tentatively assigned to this species.

LABRISOMUS (GOBIOCLINUS) BUCCIFERUS (Poey)

(Plate I Fig. 5)

Labrosomus bucciferus Poey, 1868: 399.

Labrisomus bucciferus, Jordan, 1887a: 599; Jordan and Evermann, 1896: 468; Jordan and Evermann, 1898: 2363; Nichols, 1921a: 24*; Metzelaar, 1922: 135; Jordan,

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PLATE I

Arranged Top to Bottom

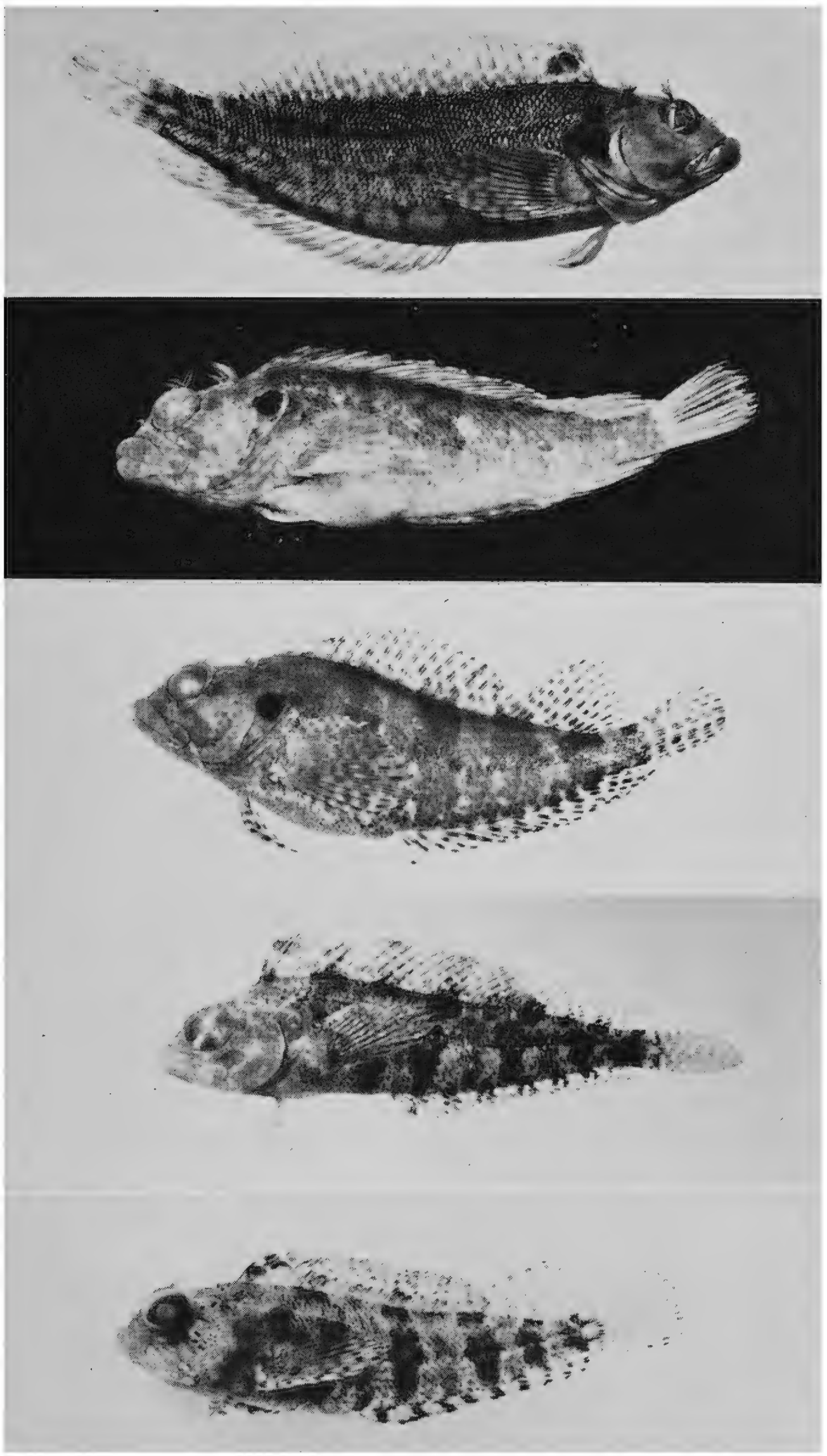
FIG. 1. *Labrisomus nuchipinnis*, UM 882, an adult male, 76.3 mm. in standard length, from Nicholstown, Andros Island, Bahamas.

FIG. 2. *Labrisomus guppyi*, CNHM 59874, an adult male, 67 mm. in standard length, from Campeche Banks, Mexico.

FIG. 3. *Labrisomus guppyi*, CNHM 61894, an adult female, 77 mm. in standard length, from Campeche Banks, Mexico.

FIG. 4. *Labrisomus haitiensis*, ANSP 74715, an adult male, 46.5 mm. in standard length, from between Periwinkle Rocks and Rose Island, Bahamas.

FIG. 5. *Labrisomus bucciferus*, ANSP 74562, an adult female, 45.3 mm. in standard length, from Rose Island, Bahamas.



Evermann, and Clark, 1930: 459; Longley, 1932: 300 (in part); Longley, 1933: 294 (in part); Longley and Hildebrand, 1941: 254; Fowler, 1944: 472; Fowler, 1950: 85 and 92; Fowler, 1953: 69; Manter, 1954: 338*; Hubbs and Springer, 1954; 348; Springer and Bullis, 1956: 97*.

Labrisomus nuchipinnis, Rosen, 1911: 66 (part not of Quoy and Gaimard); Fowler, 1936: 1037 (part not of Quoy and Gaimard).

Clinus bucciferus, Metzelaar, 1919: 154.

Labrisomus heilneri Nichols, 1921b: 2.

Ctenichthys interrupta Rivero, 1936: 69; Hubbs and Springer, 1954: 349.

Labrisomus herminier, Schmitt and Schultz, 1940: 9 (not of Le Sueur).

Ericteis kalisherae, Herre, 1942: 15 (not of Jordan).

Labrisomus gobio, Fowler, 1947: 8 (not of Valenciennes).

Description. Fin rays: dorsal XIX, 11 or 12; XX, 10 to 12; or XXI, 10 (XX, 11 in 80 percent of specimens); anal II, 19 to 21 (20); pectorals 12 to 14 (13). Lateral line 45 to 48. Gill-rakers 11 to 14.

Head 30 to 35 percent of standard length (usually 31 to 32 percent) in specimens over 30 mm. Bony orbital diameter always greater than snout length. First dorsal spine always exceeding 10.5 percent of standard length; always longer than third, fourth, fifth, penultimate, and ultimate spines. Length of shortest pelvic ray contained 1½ to 1⅘ times in longest. Interspace between bases of nuchal cirri contained ½ to 1 time in a single base. Maxillary 14.4 to 19.0 percent of standard length. Largest specimen 70 mm.

Sexual dimorphism of color pattern is restricted primarily to the fins. In the female all the fins are profusely spotted. In males, the pectorals, caudal, soft dorsal, and posterior anal are clear. The pelvics, spinous dorsal, and anterior anal fins of males are shaded with dusky of varying darkness.

All specimens have the five bands of the body extending onto the bases of the dorsal elements, and membranes of the first three dorsal spines are more heavily marked than any of the others. The body bands are lighter below the midline. The interspaces between the bands are lighter and wider than the bands. The ventral areas of the head and body are not conspicuously marked. The head is variably dusky. There are two dark lines or bars behind the eye, between which is a lighter bar.

Young of 18 to 19 mm. may be unmarked, except for a few large chromatophores atop the head and at the bases of the soft elements of the dorsal and anal. Other young of 17 mm. may already show banding of the body, and a slightly greater body depth. It is possible that the young undergo a metamorphosis, becoming shorter and stubbier when they change from a planktonic to a sedentary life. A similar type of change is indicated in *L. nuchipinnis* (*q.v.*).

Relationship. Labrisomus bucciferus is most closely related to *L. gobio*, *L. guppyi*, and *L. kalisherae*. Its uniformly dark peritoneum and low scale count serve to separate it from all *Gobioclinus*. Young of this species are often confused with *L. gobio*, but the anal fin of the latter species, when young, is only lightly marked, and the lines behind the eye are rarely noticeable.

Material. Two hundred twenty-nine specimens were examined. One hundred thirteen from the Bahamas: AMNH 7769 (holotype of *L. heilneri*), ANSP 72239–40, 72228–37, 74467, 74469, 74471, 74475, 74508, 74652, BMNH 1939.4.19.38, UM 847, 883; 80 from Cuba: MCZ 34151 (holotype of *Ctenichthys interrupta*), UM 48, USNM 82527–30,

107382, 107413–14; 7 from Puerto Rico: UMMZ 171188, 171200, 171205, 171212, 171229, 171237; 6 from the Virgin Islands: USNM 114754, 117441, UZMK P76256, 76249–50, 42; 14 from Barbados: ANSP 74463, 74465, SU 37268, USNM 86751; 1 from Old Providence Island: USNM 107113; 4 from St. Andrews Island: ANSP 72686; 1 from British Honduras: CNHM 39826; 1 from the Cayman Islands: BMNH 1939.5.12. 176–178; 1 from Swan Island: MCZ 30771; 1 from Bermuda: CNHM 48172.

LABRISOMUS (GOBIOCLINUS) GUPPYI (Norman)

(Plate I, Figs 2 and 3)

Labrisomus nuchipinnis, Rosen, 1911: 66 (part not of Quoy and Gaimard); Fowler, 1950: 85 (not of Quoy and Giamard); Springer, 1955b: 70 (not of Quoy and Gaimard).

Clinus herminier, Metzelaar, 1919: 153 (not of Le Sueur).

Clinus guppyi Norman, 1922: 533.

Labrisomus heilneri, Parr, 1930: 126 (not of Nichols).

Malacoctenus bucciferus, Fowler, 1930: 275 (not of Poey).

Malacoctenus bondi Fowler, 1930: 275.

Labrisomus guppyi, Longley and Hildebrand (in part), 1941: 254.

Starksia sanctiandrewsi Fowler, 1950: 91.

Description. Fin rays: dorsal XVIII, 11 or 12; XIX, 10 to 12 (XIX, 11 in 84 percent of specimens); anal II, 18 to 20 (19); pectorals 12 to 14 (13). Lateral line 48 to 53 (49 to 51). Gill-rakers 12 to 15 (13 or 14).

Head 31.0 to 35.7 percent of standard length in specimens over 28 mm. Bony orbital diameter rarely less than snout length. First dorsal spine rarely exceeding 10 percent of standard length; usually exceeding only third and penultimate spines. Length of shortest pelvic ray contained 1¼ to 1⅔ times in longest. Interspace between nuchal cirri bases contained 1 to 2 times in a single base. Maxillary 15.2 to 17.5 percent of standard length. Largest specimen 88 mm.

Color pattern varies with sex. Females have all the fins heavily spotted and exhibit five or six distinct bands on the body. The bands extend onto the bases of the dorsal elements. The areas between the bands are mottled, as are the head and ventral regions. There is a dark ocellus present on the opercle and usually a clear bar extending posteriorly from the eye.

In contrast to the females, the males usually have the dorsal, anal, and caudal mostly clear or only faintly marked. The pelvics and pectorals are lightly spotted. The bands on the body are usually less conspicious, except in young specimens, and the body is more uniform in color than in females. The head may be mottled. There is a dark ocellus on the opercle, and indications of a light bar extending posteriorly from the eye can usually be discerned.

Specimens at 18 mm. show the well-developed opercular ocellus and the body bands.

Discussion. The type material of *Starksia sanctiandrewsi* Fowler, here included in synonymy for the first time, consists of small specimens of this species. Fowler's aberrant counts are taken from damaged fins.

Relationship. This species is most closely related to *L. gobio* and *L. kalisherae*. It can be differentiated from these by those characters given in the key (also see *Relationship* under *L. kalisherae*). In large specimens the large teeth behind the villiform teeth in the upper jaw may approach the large size of those teeth in *L. dendriticus*.

Material. One hundred specimens were examined. Forty-seven from the Bahamas: AMNH 18288, ANSP 74677–79 (including one stained). UM 1297: 14 from Cuba: USNM 114756–58, 82532, 82533: 5 from the Virgin Islands: ANSP 74680, USNM 117426, UZMK 43, P76251–2; holotype of *M. bondi* from Grenada: ANSP 52504; 1 from Barbados: ANSP 74681; 4 paratypes of *S. sanctiandrewsi* from St. Andrews Island: ANSP 71782–5; 3 from Old Providence Island: ANSP 72685, USNM 117455; 1 from Swan Island: BMNH 1908.7.6.25; 1 from Cayman Islands: BMNH 1939.5.12. 177; and 23 from Campeche Banks, Mexico: CNHM 46655, 59874, 61894.

LABRISOMUS (GOBIOCLINUS) KALISHERAE (Jordan)

(Plate II, Fig. 1)

Ericteis kalisherae Jordan, 1904: 543; Jordan and Thompson, 1905: 254; Jordan, Evermann, and Clark, 1930:460.
Clinus bucciferus, Metzelaar, 1919: 154 (part not of Poey).
Labrisomus bucciferus, Longley, 1932: 300 (part not of Poey).
Labrisomus kalisherae, Longley and Hildebrand, 1941: 252; Springer, 1955b: 70.
Labrisomus guppyi, Longley and Hildebrand, 1941: 256 (part not of Norman).

Description. Fin rays: dorsal XVIII, 11 or 12; XIX, 10 to 12; or XX, 10 or 11 (XIX, 11 in 85 percent of specimens); anal II, 18 to 20 (19); pectorals 13 or 14 (13). Lateral line 48 to 53. Gill-rakers 10 to 13 (11).

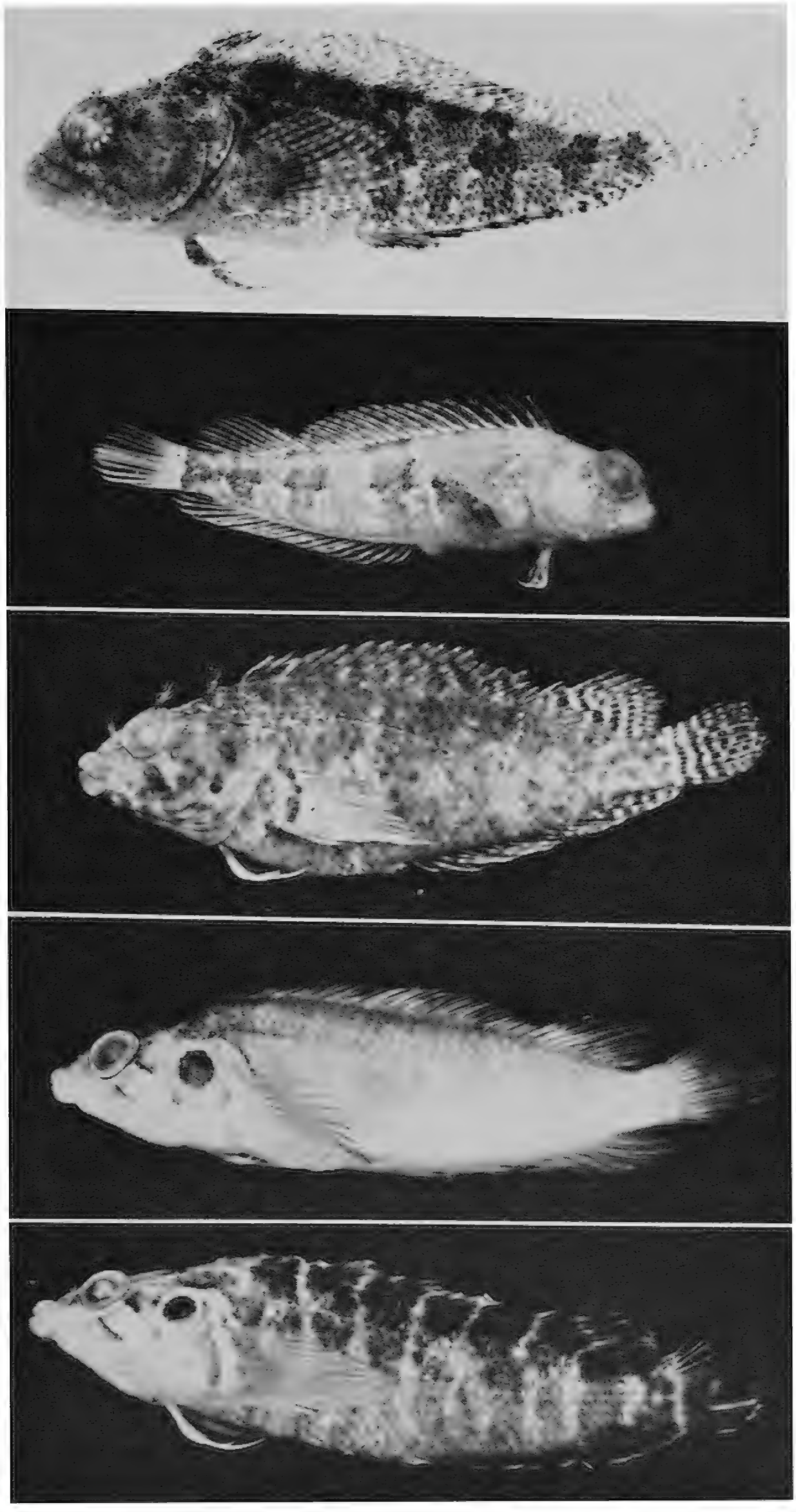
Head 31.5 to 35.8 percent of standard length in specimens over 33 mm. Bony orbital diameter always greater than snout length (orbital diameter rarely less than 10 percent of standard length; snout length rarely more than 10 percent, usually 7 to 9 percent). First dorsal spine usually more than 10 percent of standard length; always longer than third, fourth, or penultimate spines. Length of shortest pelvic ray contained 1½ to 1⅗ times in longest. Interspace between nuchal cirri bases contained 1 to 2 times in a single base. Maxillary 15.1 to 18.9 percent of standard length. Largest specimen 68.8 mm.

No differences in color pattern between males and females were noted in this species. All of the fins are densely spotted, but the spotting is not as pronounced as that in females of *L. guppyi*. The bands on the body are distinct and extend faintly onto the dorsal. The areas between the bands are lighter and broader than the bands. The head may be light or with chromatophores. There are indications of a light bar extending posteriorly from the eye. The opercle is dusky to clear, but the young have a distinct blotch in this area, which makes them resemble closely the young of *L. guppyi*. The ventral areas are uniformly dusky or light.

PLATE II

Arranged Top to Bottom

FIG. 1. *Labrisomus kalisherae*, CNHM 59877, an adult male, 66.3 mm. in standard length, from Campeche Banks, Mexico.
FIG. 2. *Labrisomus gobio*, ANSP 74712, an adult female, 40.5 mm. in standard length, from Hog Island, Bahamas.
FIG. 3. *Labrisomus albigenys*, CNHM 59875, an adult female, 51 mm. in standard length, from Campeche Banks, Mexico.
FIG. 4. *Labrisomus nigricinctus*, ANSP 74708, an adult male, 51 mm. in standard length, from New Providence Island, Bahamas.
FIG. 5. *Labrisomus nigricinctus*, ANSP 74708, an adult female, 53 mm. in standard length, from New Providence Island, Bahamas.



Discussion. There has been considerable confusion among workers as to the location of the holotype of this species. Jordan (1904) originally gave the holotype a Stanford catalogue number. Later he presented the holotype to the U.S. National Museum, where the specimen still bears the Stanford number on a metal tag in addition to the National Museum number. Longley and Hildebrand (1941) give data on the "type" of *E. kalisherae* in the British Museum. As this specimen was a gift from its collector, Thompson (British Museum, personal communication), it must be considered the same as that specimen mentioned by Jordan in his original description as being retained by Thompson. Although labeled a holotype in the British Museum, this specimen can be considered only paratypic.

Relationship. This species is most closely related to *L. guppyi* and *L. gobio*, and can be distinguished from them by those characters given in the key. Some confusion arises as to the identification of specimens of less than 40 mm. of *L. guppyi* and *L. kalisherae.* Specimens of *guppyi* may have one or two symphysial pores at this size, but always have more at larger sizes. *Labrisomus kalisherae* never has more than two symphysial pores, but it may have the opercle with a dark splotch in small specimens. In those specimens which overlap in gill-raker count, *kalisherae* can usually be distinguished from *guppyi* as the opercle blotch is less dark and sharply defined.

Material. Sixty-eight specimens were examined. One from Biscayne Bay, Florida: CNHM 50247; 37 from Tortugas, Florida and vicinity: ANSP 74682, USNM 79275 (holotype of *E. kalisherae*), 116813, and one USNM with no number; 1 from Tobago: BMNH 1931.12.5.365; 2 from Isla Fernando Noronha (Brazil); BMNH 1888.1.19. 100–101; 1 from British Honduras: USNM 49151; 21 from Compeche Banks, Mexico: CNHM 59877, 61892; 5 from Cabo Rojo, Vera Cruz, Mexico: IMSC no numbers.

LABRISOMUS (GOBIOCLINUS) GOBIO (Valenciennes)

(Plate II, Fig. 2)

Clinus gobio Valenciennes (in Cuvier and Valenciennes), 1836: 395 (in part); Storer, 1846: 372 (in part); Günther, 1861b: 276 (in part).

Labrisomus gobio. Swainson, 1839 (in part); Longley and Hildebrand, 1941: 257; Hubbs and Springer, 1954: 348.

Gobioclinus gobio, Gill, 1860b: 277 (in part); Jordan 1887a: 599 (in part); Jordan and Evermann, 1896: 468 (in part); Jordan and Evermann, 1898: 2365 (in part); Jordan, Evermann, and Clark, 1930: 455 (in part); Hubbs, 1952: 102 (in part); Hubbs and Springer, 1954: 346.

Labrisomus heilneri Nichols, 1921b: 2 (in part: paratype).

Description. Fin rays: dorsal XVIII, 12; XIX, 10 to 12; or XX, 10 or 11 (XIX, 11 in 77 percent of specimens); anal II, 18 to 20 (19); pectorals 12 or 13 (13). Lateral line 48 to 53 (49 to 51). Gill-rakers 11 to 14 (13 or 14).

Head 29 to 31 percent of standard length in specimens over 25 mm. Bony orbital diameter always more than 10 percent of standard length (usually more than 11 percent); always considerably greater than snout length, which is rarely more than 8.7 percent and always less than 10 percent of standard length. First dorsal spine about 10 percent of standard length; always exceeding penultimate spine, and always shorter than fourth and fifth spines. Length of shortest pelvic ray contained 1½ to 1⅔ times in longest. Interspace between nuchal cirri bases contained ½ to 1⅓ times in

a single base. Maxillary 12.4 to 16.1 percent of standard length (usually more than 14 percent). Largest specimen 49.2 mm.

This species is the least strongly marked of all *Labrisomus*. Except for a light specking of the dorsal, anal, and caudal fins of females, there is no difference in color pattern between the sexes. All the fins of the male are clear, as are the pelvics and pectorals of the female. There are five bands on the body which may extend just to the bases of the dorsal elements. They are about the same width as the areas between them. The bands are darker than the interspaces, which have a light color covered by dusky markings. The ventral areas of the head and body are light and unmarked. The head is usually unmarked, but has some diffusely marked areas on the cheek.

Relationship. This species is most closely related to *L. guppyi* and *L. kalisherae* and can be distinguished from them by those characters given in the key.

Material. Seventy-six specimens were examined. Sixty-four from the Bahamas: AMNH 7769 (paratype of *L. heilneri*), ANSP 72238, 74455, 74457–8, 74468, 74474, 74476. 74660, 74712 (including one stained), UM 844; 10 from Cuba: USNM 82531. 114753; 1 from the Virgin Islands: ANSP 74473; 1 from Belize, British Honduras: USNM 91817.

LABRISOMUS (GOBIOCLINUS) ALBUQUERQUENSIS (Fowler) nomen dubium
Malacoctenus albuquerquensis Fowler, 1944: 162 and 243; Fowler, 1953: 69.

The holotype and paratype (ANSP 69987 and 69988) of this nominal species represent post-larval stages of either one or two of the following: *L. gobio*, *L. kalisherae*, or *L. guppyi;* all of which have priority over *L. albuquerquensis.* Present knowledge of life histories of these species is not complete enough to enable exact identification.

LABRISOMUS (BROCKIUS) ALBIGENYS Beebe and Tee Van
(Plate II, Fig. 3)

Labrisomus albigenys Beebe and Tee Van, 1928: 233; Fowler, 1952: 105.

Description. Fin rays: dorsal XVIII, 11; anal II, 18; pectorals 13. Lateral line 41 to 44. Gill-rakers 13 or 14.

Head 33.4 to 34.4 percent of standard length in specimens over 47 mm. Bony orbital diameter less than snout length in specimens over 47 mm. First dorsal spine less than 8 percent of standard length; usually shorter than any other dorsal spine, except penultimate, which it may exceed. Length of shortest pelvic ray contained approximately 2 times in longest. Interspace between nuchal cirri bases contained ⅘ to 1 1/10 times in a single base. Maxillary 12.2 to 13.4 percent of standard length. Largest specimen 52.4 mm.

Color pattern is slightly different in males and females. Females have the dorsal. anal, and caudal fins with several rows of dark spots. There are faint indications of about eight stripes on the dorsal portion of the body which extend onto the dorsal fin. The pelvics are light with dusky bases. The ground color of the body is a uniform dusky brown with scattered darker spots. The venter is light brown. There is a distinct dark stripe at the bases of the pectoral rays followed by a light stripe on the prepectoral area. The ground color of the head is about as dark as that of the body. The opercle has some dark spots with light areas between them. The underside of the head is alternately barred or mottled with dark and light. There are two bands leading posteroventrally from the eye with a light bar between them.

The male examined is more uniform in color. Faint spots are present only on the caudal. The anal is dusky. The pectorals, pelvics, and ground color of the body are the same as in the females. The head, however, is uniformly dusky below and the posteroventral bars leading from the orbits are not so obvious.

Photographs of the holotype, when fresh, indicate that this small specimen was somewhat intermediate in coloration between males and females, with a more pigmented spinous dorsal than any of the adults.

Discussion. This species is, at present, the most poorly represented of its genus in museum collections. The considerable distance between the two localities from which it is known indicates that it is probably widely distributed, and future collecting will probably establish this.

The holotype is at present in very poor condition and will probably be valueless for study in another few years. Two excellent photographs taken of the holotype were kindly given to me by Dr. John Tee Van, and these have been deposited in the U.S. National Museum.

Relationship. This species is most closely related to *L. striatus* and *L. nigricinctus.* It differs from the former mainly in not having scales on the cheek, and the latter in the nature of its coloration.

Material. Five specimens were examined. The holotype, NYZS 7372, from Port-au-Prince Bay, Haiti, and four specimens, CNHM 59875, from Cayos Arcos, Campeche Banks, Mexico.

LABRISOMUS (BROCKIUS) NIGRICINCTUS Rivero

(Plate II Figs. 4 and 5)

Labrisomus nigricinctus Rivero, 1936: 68.
Starksia oculata Fowler, 1947: 9; Fowler, 1950: 92.

Description. Fin rays: dorsal XVII, 11; XVIII, 10 to 12; or XIX, 11 (XVIII, 11 in 90 percent of specimens); anal II, 17 to 20 (18 in 86 percent of specimens); pectorals 13. Lateral line 40 to 44 (41 or 42). Gill-rakers 9 to 12 (10 or 11).

Head usually 29 to 31 percent of standard length in specimens over 30 mm. Bony orbital diameter usually greater than snout length. First dorsal spine always less than 8 percent of standard length; shorter than any other dorsal spine, except penultimate which it occasionally equals. Length of shortest pelvic ray contained 1⅘ to 2¼ times in longest. Interspace between nuchal cirri bases contained ⅘ to 1⅘ times in a single base. Maxillary 10.2 to 12.1 percent of standard length. Largest specimen 53.6 mm.

Color pattern is dependent upon age and sex. Females and young males have about eight or nine broad, dark bands separated by narrow light stripes. The first two bands are on the caudal. Bands and stripes on the body extend onto the dorsal and anal, and are most distinct on the dorsal. The pectorals are light with a dusky area at the base of the rays, followed by a light band and another dusky band on the prepectoral area. The pelvics are clear and other portions of the ventral region are light. The fins although barred are never spotted. There is a well-developed ocellus on the opercle, and two thin, dark lines leading posteroventrally from the eye with a broad, light band between them. A similar light band bordered by dusky areas extends anteroventrally from the eye across the maxillary.

Adult males are uniformly light with some dusky markings on the body and fins. The

opercular ocellus, bands on the prepectoral region, and those on the head are as in the female. The opercular ocellus is present in specimens 12.6 mm. in standard length.

Discussion. The holotype of *S. oculata* Fowler is a typical specimen of Rivero's species.

Relationship. This species is most closely related to *L. striatus* and *L. albigenys.* It differs from both of these in having a well-developed opercular ocellus, in the solid barring, but never spotting, of the soft dorsal and caudal, in the nature of its striking sexual dimorphism of color pattern, in having a slightly shorter jaw, and in having fewer gill-rakers. In addition to these characters it differs from *L. striatus* in not having scales on the cheeks.

Material. Sixty-one specimens were examined. One from Sand Key, Florida: ANSP 74516; 38 from the Bahamas: ANSP 71735 (holotype of *Starksia oculata*), 74472, 74708, 72306–09, 74512–15, 74622 (including one stained), 74623; 8 from Cuba: MCZ 34150 (holotype of *L. nigricinctus*), USNM 130790, 82538–40; 1 from the Virgin Islands: UZMK 44; 13 from Barbados: ANSP 74517–18, 74624.

MALACOCTENUS Gill

Malacoctenus Gill, 1860b: 103 (type *Clinus delalandii* Valenciennes, in Cuvier and Valenciennes, 1836, by original designation).

Acteis Jordan, 1904: 543 (type *Malacoctenus moorei* Evermann and Marsh, 1900a, by original designation).

Description. Fin rays: dorsal XVIII, 10 to 12; XIX, 9 to 13; XX, 9 to 14; XXI, 8 to 13; XXII, 8 to 13; XXIII, 9 to 10 or 13; anal II, 17 to 24; caudal 13; pectorals 13 to 17; pelvics I, 3.

Lateral line 40 to 66; scales on anterior half of posterior arc with anterior pore exposed or not. Head naked. Fin membranes naked. Prepectoral area and breast naked to completely scaled.

Jaws with a single row of large conical teeth (except *M. erdmani* with four or five small teeth behind the outer row, *M. macropus* with teeth biserial, and *M. boehlkei* with a patch of villiform teeth behind the large outer row). Vomerine teeth present. Palatine teeth absent.

Gill-rakers 8 to 15 on first arch.

Origin of dorsal fin in region above opercle. Length of spinous dorsal longer than that of soft dorsal. Penultimate dorsal spine shorter than ultimate. Soft dorsal higher than spinous dorsal, except in occasional specimens where the anterior two spines may approach the soft dorsal height. Soft dorsal free from caudal (except *M. boehlkei, M. macropus, M. erdmani,* and *M. gilli* with the soft dorsal bound to caudal base).

Anal, caudal, pectorals, and pelvics as in *Labrisomus.*

Distribution of cirri same as in *Labrisomus.* Interspace between nuchal cirri bases frequently contained more than three times in a single base.

Maxillary 7.9 to 11.2 percent of standard length (usually 8.5 to 9.5, and rarely more than 10.1 percent). Maxillary almost completely sheathed by preorbital.

A hook sometimes present on anterior margin of cleithrum in specimens of *M. erdmani* and *M. aurolineatus.*

Color pattern is distinct in many of the species and is most useful in identifying the young; however, specimens of one species may show color patterns similar to those of unrelated species (i.e. *M. triangulatus* and *M. boehlkei*).

Sexual dimorphism. Urinogenital openings as in *Labrisomus*.

There is no difference between males and females in the size of the jaws. Secondary sexual dimorphism in pigmentation may be like that found in *Labrisomus*, or the males may have the increased pigmentation, but without spotting. In rare instances mature females will exhibit male-type coloration; and in some populations of *M. triangulatus* males and females will exhibit only male-type coloration.

In *M. macropus*, *M. erdmani*, *M. gilli*, and *M. aurolineatus* sexually ripe males develop large fleshy pads on the innermost pelvic ray.

Adult males are usually more completely scaled on the ventral areas than females. Frequently females do not develop scales in the breast region. The scales in the ventral areas of males often become fleshy and raised, increasing in degree from anterior to posterior.

Phylogeny. Malacoctenus is considered to have branched off close to the stock which gave rise to the subgenus *Brockius*. The most primitive species of the genus are considered to be those with high pectoral counts and increased dentition. Relationships within the genus are indicated under the appropriate heading within the species descriptions, but are to be considered only tentative.

Jordan (1904) erected the genus *Acteis* to include *Malacoctenus macropus* (actually its synonym *M. moorei*) based upon differences in dentition and pectoral counts from other species of *Malacoctenus*. The fact that there is a gradation from no teeth behind the outer row in *M. margaritae* to a patch of teeth behind the outer row in *M. boehlkei* tends to negate the importance of teeth in segregating the four species with higher pectoral counts from the other members of the genus. The higher pectoral count does, however, serve to set these species apart; but even so, specimens with higher pectoral counts are occasionally found among the other species. In addition to this, the similarity of the unique sexual dimorphism of males between *M. macropus* and *M. erdmani*, and between *M. gilli* and *M. aurolineatus*, convinces me that differentiation has not proceeded far enough to merit the erection of separate genera.

In order to facilitate identification, separate keys are given for the Atlantic and Pacific species; also, it seems that the Atlantic and Pacific forms are more closely related intrageographically than intergeographically.

KEY TO THE PACIFIC SPECIES OF MALACOCTENUS

(N) = North of Latitude 15° N
(S) = South of Latitude 13° N

A. Pectoral rays 15 or more in 98 percent of specimens; scales on venter same size as those on sides ..... *M. margaritae* (p. 448)

(A). Length of shortest pelvic ray usually contained more than 2¼ times in longest; symphysial pores more (Table 2); scale rows between anterior lateral line and dorsal contour usually 3, sometimes 4 (Table 2) ..... (S) *M. m. margaritae* (p. 449)

(AA). Length of shortest pelvic ray usually contained less than 2¼ times in longest; symphysial pores less; scale rows between anterior lateral line and dorsal contous usually 4, sometimes 5 ..... (N) *M. m. mexicanus* (p. 449)

AA. Pectoral rays usually 14; scales on center reduced in size ..... B

B. Total dorsal elements 33 or more in 94 percent of specimens; interspace between nuchal cirri bases contained one time or less in a single base ..... (N) *M. gigas* (p. 457)

BB. Total dorsal elements less than 33 (33 or more in less than 1 percent of specimens of *M. hubbsi*, which is sympatric with *M. gigas*, and in less than 7 percent of specimens of *M. zonogaster*, which occurs only in the Galapagos); interspace between nuchal cirri bases contained more than one time in a single base (9/10 to 1 time in less than 6 percent of specimens of *M. hubbsi*) C

C. Dorsal spines 21 or 22 in more than 98 percent of specimens; a dark round blotch covering upper half of opercle and appearing in line with a series of dark blothches which occur in the middle of each body band ..... (S) *M. zonogaster* (p. 472)

CC. Dorsal spines 18 to 20 (21, never more, in less than 5 percent of specimens; never 21 in *M. afuerae* or *M. costaricanus*); no such blotch on upper half of opercle ..... D

D. At least one scale on midline anterior to first dorsal spine (it may be impedded; not valid for specimens of *M. zonifer* of less than 25 mm.) ..... E

DD. No scales on midline anterior to first dorsal spine ..... G

E. Preopercular canals rarely extending more than one-third (never more than two-fifths) distance across opercle; length of shortest pelvic ray contained usually less than 1¾ times in longest ..... *M. zonifer* (p. 474)

(E). Membranes of anterior dorsal spines with a dark splotch dorsally; symphysial pores more (Table 8) ..... (S) *M. z. sudensis* (p. 474)

(EE). Membranes of anterior dorsal spines without a dark splotch dorsally; symphysial pores less (Table 8) ..... (N) *M. z. zonifer* (p. 474)

EE. Preopercular canals usually extending one-half distance or more across opercle; length of shortest pelvic ray contained usually more than 1¾ times in longest ..... F

F. First dorsal spine less than 10.5 percent of standard length; dorsal spines usually 20; anal rays usually 20; interspace between nuchal cirri bases contained less than 3 times in a single base; symphysial pores 1 or 2 ..... (N & S) *M. ebisui* (p. 478)

FF. First dorsal spine more than 11 percent of standard length; dorsal spines 19 (only 4 specimens known); anal rays 19; interspace between nuchal cirri bases contained more than 3½ times in a single base; symphysial pores 4 or more ..... (S) *M. costaricanus* (p. 468)

G. Peritoneum white, sometimes with scattered large chromatophores; first dorsal spine usually less than 10 percent of standard length ..... *M. afuerae* (p. 461)

(G). Entire fish suffused with numerous spots of varying sizes (Plate V Fig. 5) ..... (N) *M. a. multipunctatus* (p. 426)

(GG). Body more uniform in color; spots never on venter (Plate V Fig. 4) ..... (S) *M. a. afuerae* (p. 462)

GG. Peritoneum almost uniformly stippled with chromatophores (most dense dorsally); first dorsal spine usually more than 10 percent of standard length ..... H

H. A spot or blotch at the base, or just anterior to the base, of each pelvic fin (rarely absent in adults; rarely present in young under 40 mm.); prepectoral area with or without scales; interspace between nuchal cirri bases contained usually

less than 3 times in a single base; anal rays 19 to 21 (18 in one specimen out of over 1200; less than 50 percent of specimens with 19); attaining a length of 79.5 mm. ..... (N) *M. hubbsi* (p.)

(H). Lateral line scales modally 54 to 56 (Table 5); symphysial pores less (Table VI) ..... *M. h. hubbsi* (p. 465)

(HH). Lateral line scales modally 51 to 53 (Table 5); symphysial pores more (Table VI) ..... *M. h. polyporosus* (p. 468)

HH. Markings at base of pelvic fins present in only 2 out of 67 specimens; prepectoral area never scaled; interspace between nuchal cirri bases contained 3 or more times in a single base; anal rays 18 or 19 (20 in 1 of 67 specimens); largest specimen 47 mm. ..... (N) *M. zacae* (p. 470)

KEY TO THE ATLANTIC SPECIES OF MALACOCTENUS

(W) = Western Atlantic
(E) = Eastern Atlantic

A. Length of shortest pelvic ray contained four or more times in longest; a patch of small teeth anteriorly behind the large outer row in each jaw; pectoral rays usually 15 ..... (W) *M. boehlkei* (p. 443)

AA. Length of shortest pelvic ray contained less than four times in longest; small teeth, when present, in a single row behind the large outer row; pectoral rays 14 to 17 ..... B

B. Pectoral rays typically 15 to 17; scales on prepectoral area, if present, about same size as those on body; small teeth present behind large outer row[1] C

BB. Pectoral rays typically 14; scales on prepectoral area, if present, reduced in size; small teeth never present behind large outer row ..... D

C. Pectoral rays 15 to 17 (usually 16); pectoral base never scaled; small teeth behind large outer row never more than 5 in each jaw; interspace between nuchal cirri contained ½ to 1⅛ times in a single base; a distinct black blotch at bases of last dorsal spines (most prominent color marking) probably only rarely exceeding 30 mm. in standard length ..... (W) *M. erdmani*[1] (p. 444)

CC. Pectoral rays 14 to 16 (usually 15); pectoral base rarely without scales; small teeth present as a series of more than 6 teeth behind each large outer row; interspace between bases of nuchal cirri contained less than ½ time in a single base; no outstanding black blotch at bases of last dorsal spines; frequently exceeding 40 mm. in standard length ..... (W) *M. macropus* (p.???)

D. At least one scale on midline before first dorsal spine (it may be imbedded); color pattern primarily of three to five inverted triangles on sides of body; prepectoral area scaled ..... (W) *M. triangulatus* (p. 477)

DD. No scales on midline before first dorsal spine; color pattern otherwise; prepectoral area scaled or not ..... E

E. Most prominent color markings a dark ocellus on anterior dorsal spines and another on sides of body and bases of posterior dorsal spines; scales on venter, when present, same size as those on sides; prepectoral area without scales; soft dorsal closely bound to caudal base ..... (W) *M. gilli* (p. 450)

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[1] Because of the very small size of *M. erdmani* and the fragility of the teeth behind the outer row, these teeth are frequently lost when a needle is inserted into the mouth of a specimen. It is only with difficulty that they can be seen.

EE. Color markings otherwise; scales on venter, when present, reduced in size; prepectoral area with or without scales; soft dorsal free from caudal base ..... F

F. Lateral line scales more than 56; scales usually present on prepectoral area; stripes on body extending almost to tips of dorsal spines without diminution....G

FF. Lateral line scales less than 56; scales never present on prepectoral area; stripes on body changed considerably in appearance on dorsal; not extending more than ½ distance up dorsal spines ..... H

G. Dorsal spines 18 (28 specimens examined); at least one (usually 3) preopercle canal extending well onto opercle ..... (W) *M. versicolor* (p. 455)

GG. Dorsal spines 20 (1 specimen examined); preopercle canals scarcely encroaching on opercle ..... (E) *M. africanus* (p. 456)

H. Membranes in region of first 3 dorsal spines more darkly pigmented than others; interspaces between bands on body of about uniform width; no humeral blotch present; 2 canals extending from preopercle onto opercle ..... (W) *M. delalandei* (p. 460)

HH. Membranes in region of first 3 dorsal spines containing little or no pigment; not different from remaining membranes; anterior two or three bands on body separated from posterior bands by a wider space than occurs between any of the other bands; first two bands sometimes fused dorsally into a humeral blotch; 3 canals extending from preopercle onto opercle..(W) *M. aurolineatus* (p. 454)

MALACOCTENUS BOEHLKEI, New Species

(Plate III, Fig. 1)

Description. Fin rays: dorsal XX, 13; XXI, 11 or 12; or XXII, 11; anal II, 20 to 23 (22). Lateral line 58 to 66. Gill-rakers 8 to 11 (10). Symphysial pores 1 or 2 (1).

Head 26.4 to 32.2 percent of standard length in specimens over 25 mm. Bony orbital diameter 8.8 to 11.4 percent of standard length in specimens over 25 mm; smaller than snout in specimens over 45 mm. All dorsal spines, except rarely third and fourth, greater than 10 percent of standard length. First dorsal spine always shorter than tenth to last dorsal spines. Length of shortest pelvic ray contained 4½ to 11½ times in longest; 6 or more times in specimens over 40 mm.; frequently appearing to be absent. Interspace between nuchal cirri bases contained ½ to 1⅕ times in a single base. Maxillary length 8.5 to 10.7 percent of standard length; usually less than 9.3 percent. Largest specimen 50.8 mm.

Scales present on midline before dorsal, on prepectoral area, and prepelvic area in adults over 40 mm. Lateral line scales are variable in size and many of those on the posterior portion have no canals. The circuli of the body scales are more prominent than in the other species of the genus. Breast scales of males are sometimes imbedded.

There are two preopercular canals which just encroach upon the opercle.

Coloration is different in males and females. In males all the fins are clear with some scattered dusky areas on the membranes. There is an ocellus on the membranes between the second, third, and fourth dorsal spines about midway up from their bases. There are six or seven pentagonal saddle-like markings on the body with their bases on the dorsal body contour. The saddles are darker ventrally. Below each of these saddles and between the anterior ones are darker diamond-shaped marks, each of which has a clear spot in its center. These diamonds are lighter than the saddles in some specimens. On the pre-

pectoral, prepelvic, and ventral head regions there are alternating dark and light bands, which in the latter area extend onto the cheeks.

Females have the same basic color pattern as males, but are much lighter. In some cases the pattern is scarcely visible, and in all specimens the ventral areas are uniformly light.

Coloration in life, as taken from color slides kindly supplied by Dr. J. Böhlke, shows that the saddles and diamonds of males are black, margined with white. The top of the head, areas between the saddles, and the dorsal and caudal fins are yellow-brown. In females the saddles are orange-brown, and the diamonds are bright orange with white centers. The belly and the areas between the diamonds are white. The fins and head are tinged with light orange.

Discussion. Dr. J. Böhlke informs me that in contrast to other labrisominids, *M. boehlkei* is taken only in comparatively deep water: fifty feet.

Relationship. This species of *Malacoctenus* differs from all others in its extremely long pelvic fins and in the nature of its dentition. It is most closely related to *M. macropus* and *M. erdmani* in the nature of its high pectoral count and the fact that small teeth are present behind the large outer rows.

Holotype. ANSP 74719, an adult male, 42 mm. in standard length, from north of the east end of Rose Island, Bahamas (ANSP Station 292), 25° 07′ 55″ north latitude and 77° 05′ 32″ west longitude (H. O. Chart 1611/June, 1938). Collected by C. C. G. Chaplin, E. Browing, S. Waterman, and J. Böhlke, May 5, 1956.

Paratypes. Eighteen specimens. One from Sandy Cay, Bahamas: ANSP 74691; 17 from one-quarter mile north of the center of Green Cay, Bahamas: ANSP 77931–33.

I take pleasure in naming this species for Dr. J. Böhlke, who first brought a specimen to my attention and who gave considerable assistance in curatorial matters.

MALACOCTENUS MACROPUS (Poey)

(Plate III, Fig. 2)

Myxodes macropus Poey, 1868: 399; Poey, 1875: 173; Jordan, 1887a: 599; Garman, 1896: 89*.

Malacoctenus macropus, Jordan and Evermann, 1896: 467; Jordan and Evermann, 1898: 2357; Evermann and Kendall, 1900: 93; Bean, 1905: 319; Jordan, Evermann, and Clark, 1930: 460; Longley, 1932: 300; Fowler, 1941: 98; Longley and Hildebrand, 1941: 247; Fowler, 1945: 327; Fowler, 1947: 7; Manter, 1947: 295*; Fowler, 1952: 105; Kanazawa, 1952: 90; Springer, 1955b: 70; Springer and Bullis, 1956: 97; Smith, 1957: 15.

PLATE III

Arranged Top to Bottom

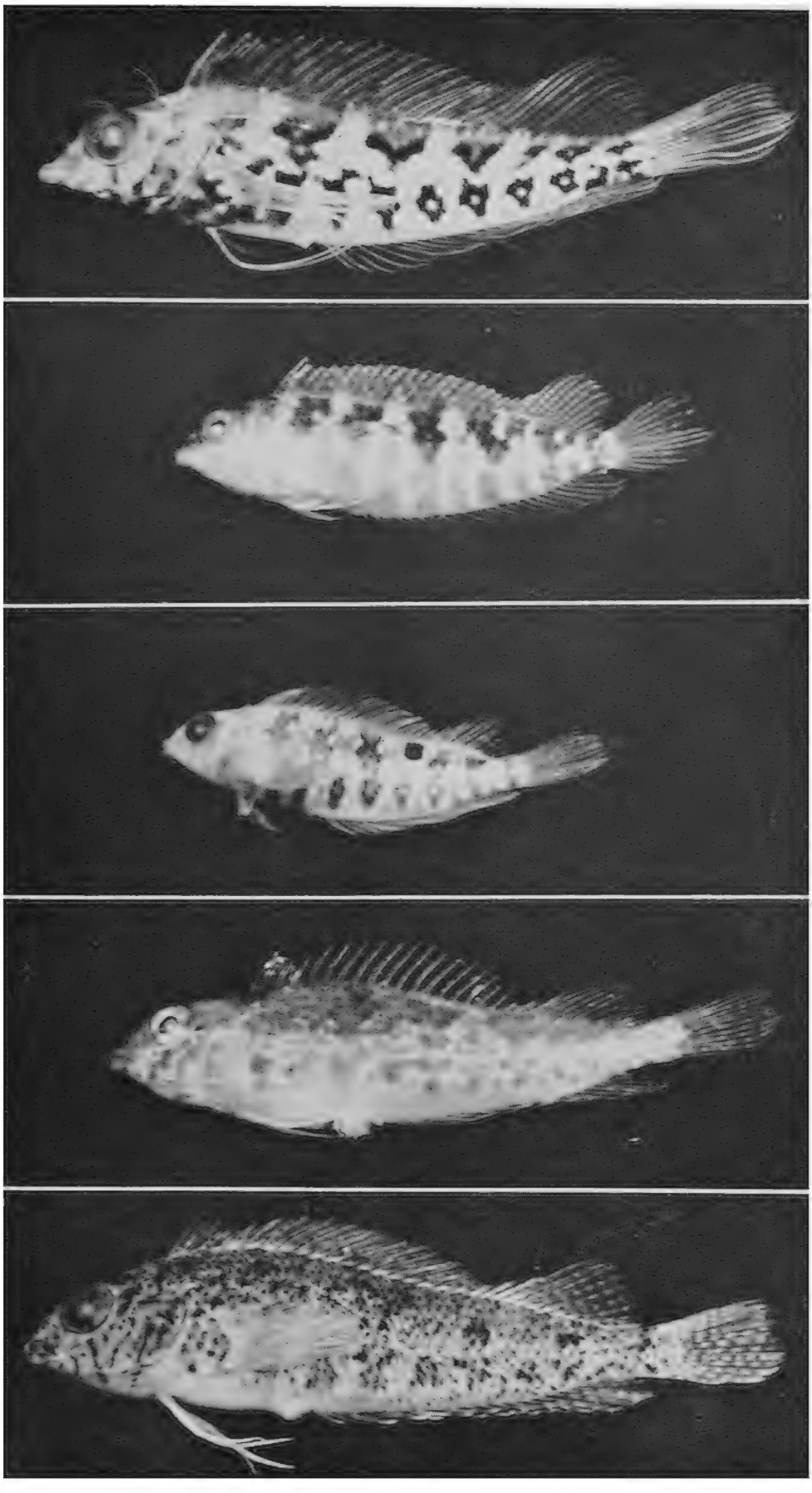
FIG. 1. *Malacoctenus boehlkei*, ANSP 74719, holotype, an adult male 42 mm. in standard length, from Rose Island, Bahamas.

FIG. 2. *Malacoctenus macropus*, ANSP 74714, an adult male, 33 mm. in standard length, from New Providence Island, Bahamas.

FIG. 3. *Malacoctenus erdmani*, ANSP 74726, an adult male, 23 mm. in standard length, from Hog Island, Bahamas.

FIG. 4. *Malacoctenus margaritae margaritae*, SU 49680, an adult female, 39.2 mm. in standard length, from the Gulf of Nicoya, Costa Rica.

FIG. 5. *Malacoctenus margaritae mexicanus*, UCLA W53–91, an adult male, 44 mm. in standard length, from Bahia Santa Inez, Baja California, Mexico.



Malacoctenus moorei Evermann and Marsh, 1900a: 358; Evermann and Marsh, 1900b: 309; Jordan and Evermann, 1900: 3188; Rosen, 1911: 67; Beebe and Tee Van, 1928: 235.

Acteis moorei, Jordan, 1904: 543; Jordan and Thompson, 1905: 254; Jordan, Evermann, and Clark, 1930: 460; Parr, 1930: 128*; Nichols, 1930: 375; Herre, 1942: 15.

Acteis macropus, Jordan and Thompson, 1905: 254.

Description. Fin rays: dorsal XXI, 9 to 11; XXII, 8 to 10; or XXIII, 9 or 10 (dorsal formula variable with population); anal II, 18 to 22 (20 or 21); pectorals 14 to 16 (15). Lateral line 40 to 45. Gill-rakers 8 to 11. Symphysial pores 1 or 2.

Head 24.5 to 28.6 percent of standard length in specimens over 25 mm. Bony orbital diameter 8 to 11 percent of standard length in specimens over 25 mm.; usually greater than snout length, occasionally equal to it. Snout length never exceeding 10 percent of standard length (usually 8 to 9 percent). First dorsal spine 11.3 to 18.8 percent of standard length (rarely less than 13 percent); always exceeding second through fifth and last four dorsal spines; frequently exceeding tenth dorsal spine. Length of shortest pelvic ray contained 2 to 3⅛ times in longest. Interspace between bases of nuchal cirri contained less than ½ times in a single base. Maxillary length 8.5 to 9.6 percent of standard length. Largest specimen 43.2 mm.

Scales not present on midline before dorsal; present on prepectoral area and breast. Last several scales of lateral line without tubes.

None of the preopercular canals extend onto the opercle.

Mature males have a large fleshy pad enveloping the innermost ray on each pelvic fin.

Sexual dimorphism of color pattern exists only for the dorsal fin, which is spotted in the areas above the bands on the body in females, and is uniformly dusky in males.

The anal and caudal fins are dusky; the pectorals and pelvics are unmarked. The body is marked by six to nine irregular bands, which are darker dorsally. Each band may divide into two on the ventral portion of the sides. The interspaces between the bands are light or dusky. The venter and ventral head regions may be light or uniformly dusky; infrequently the underside of the head is irregularly marked. The sides of the head may be light, dusky, with or without small spots.

Specimens from Campeche Banks, Mexico, are more heavily pigmented than any others which were examined.

Discussion. Collections from Campeche Banks, Mexico, have modal counts of 23 total anal elements and 32 total dorsal elements. Those from other localities have modal anal counts of 22 and modal dorsal counts of 31.

The type material of *Myxodes macropus* (MCZ 12511) consists of two specimens of approximately 31 and 25 mm. Both of these specimens are in very poor condition, but for the sake of future stability of the name, I take the opportunity here to designate the larger specimen as lectotype.

Relationship. Malacoctenus macropus differs from all other species of *Malacoctenus* in particulars of its dentition. It is most closely related to *M. boehlkei* and *M. erdmani.* It differs from the former also in having a shorter pelvic fin in the nature of its coloration, and from the latter in the nature of its scalation, coloration, size, and typical fin counts.

Material. Six hundred fourteen specimens were examined. One from Vero Beach, Florida (H56–24, Personal collection of R. W. Harrington); 10 from Miami south to

Key West, Florida: ANSP 74503, 74687, CNHM 41677–78, 50248, TNHC 3886, UM 64; 162 from Tortugas, Florida: ANSP 74501, 74686, BMNH 1933.10.12.181–7, SU 8235, UM 54, UMMZ 87963, 147736, 147788, USNM 50823, 88079, 88081–82, 92579, 114709, 114714, 116820–22, 117125, 118389, 131317, 133882–83; 34 from Cay Sal Bank, Bahamas: UM 853; 335 from the northern Bahamas: AMNH 17307, 17935, 18287, 20262, ANSP 72189, 72593–99, 74485–74500, 74571–81 (including one stained), 74714, 74720, 74731, USNM 53222–23; 4 from Cuba: MCZ 12511 (Syntypes of *M. macropus*), USNM 37430, 114704; 11 from Puerto Rico: SU 8151, UMMZ 171195, 171201, 171232, USNM 49370 (holotype of *M. moorei*), 128792; 3 from the Virgin Islands: ANSP 74502, MCZ 12632, USNM 78160; 1 from Antigua: SU 37246; 2 from the Cayman Islands: BMNH 1939.5.12.178, 1939.5.12.181; 1 from Jamaica: USNM 50898; 43 from Campeche Banks Mexico: CNHM 59876; 1 from Bermuda: CNHM 48713.

MALACOCTENUS ERDMANI Smith

(Plate III Fig. 3)

Clinus puertoricensis, Metzelaar, 1919: 152* (not of Evermann and Marsh).
Malacoctenus bimaculatus, Herre, 1942: 17 (part not of Steindachner).
Malacoctenus erdmani Smith, 1957: 8.

Description. Fin rays: dorsal XX, 9 or 10; XXI, 8 to 10; or XXII, 8 or 9 (XXI, 9 in 54 percent of specimens); anal II, 17 to 20 (18 or 19); pectorals 15 to 17 (16). Lateral line 40 to 44. Gill-rakers 8 to 10 (8 or 9). Symphysial pores 1 or 2 (1).

Head 26.8 to 30.2 percent of standard length in specimens over 17 mm. Bony orbital diameter frequently exceeding 10 percent of standard length; always larger than snout length (except possibly in holotype; see Smith, 1957) which never exceeds 10 percent of standard length. First dorsal spine always more than 10 percent of standard length (usually more than 11 percent); never exceeded by second through fifth, fourth from last, third from last, or penultimate dorsal spines; sometimes equaled by second dorsal spine; usually exceeded by tenth and last dorsal spines. Length of shortest pelvic ray contained 1⅘ to 2½ times in longest. Interspace between bases of nuchal cirri contained ½ to 1⅛ times in a single base. Maxillary length 8.3 to 11 percent of standard length (usually less than 10 percent). Largest specimen 29 mm.

Scales are not present on midline before dorsal or on prepectoral areas. They are sometimes present on the breast in males.

There are two preopercular canals which barely encroach on the opercle.

A hook is usually present on the anterior margin of the celithrum of adults.

Mature males have a large fleshy pad enveloping the innermost ray on each pelvic fin.

Coloration is dependent upon sex to varying degrees. All the fins are clear and unmarked, though some females have a very delicate spotting on the dorsal, anal, and caudal. Banding in mature males is usually more emphasized, and those bands above the venter may extend onto and across this area. The bands form very dark areas on either side of the light pelvic bases. Frequently the head is barred below with light and dark areas. Barring in females frequently is subdued, and the venter and area below the head are uniformly light.

There are indications of about eight bands on the body. These are darkest dorsally; they may be entirely interrupted or only subdued in their mid-portions, but darker

again below. The most obvious marking is a subquadrate blotch on the back at the bases of the last few dorsal spines. Infrequently the dorsal portions of the bands equal this blotch in intensity. It is probably because of this blotch and *M. erdmani*'s presence in a superimposed ecological habitat (Smith, 1957), that it is confused with *M. gilli.*

Additional lighter bands are often indicated in the interspaces between the bands below the midline of the body.

The sides of the head are variably dusky.

Specimens of 12 mm. show indications of adult coloration.

Discussion. Of 15 specimens from Cuba, two had 19, ten had 20, two had 21, and one had 22 total anal elements. These frequencies indicate a possible difference from populations in the Bahamas. Of 51 specimens from the Bahamas, three had 19, 14 had 20, 32 had 21, and two had 22 total anal elements. Of 18 specimens from Puerto Rico, nine each had 20 and 21 total anal elements.

From the published description of Metzelaar's (1919) material from Curaçao, it would appear that he had this species. Herre's (1942) specimens were examined and found to consist of a mixture.

Relationship. This species is most closely related to *M. boehlkei* and *M. macropus.* It differs from both of these in the nature of its dentition, which is decreased, and in its typical fin ray counts.

Material. Ninety-nine specimens were examined. Sixty-three from the Bahamas: ANSP 74461–62 (including one stained), 74509–10, 74695–98, 74725–27 (and 12 uncatalogued specimens bearing Lot number 282), UM 891, USNM 114707; 18 from Cuba: USNM 107415–16, 114707, 82543, 82541; 17 from Puerto Rico (paratypes): UMMZ 171157, 171173, 171176, 171183, 171187, 171192, 171204, 171207, 171211, 171217, 171226, 171231; 1 from Barbados: SU 49616.

MALACOCTENUS MARGARITAE (Fowler)

(For synonymy see subspecies)

Description. Fin rays: dorsal XX, 12; XXI, 10 to 12; or XXII, 11 (XXI, 11 in 85 percent of specimens); anal II, 20 to 22 (21); pectorals 14 to 16 (15). Lateral line 51 to 56. Gill-rakers 10 to 12. Symphysial pores 1 to 4.

Head 25.4 to 27.9 percent of standard length in specimens over 30 mm. Bony orbital diameter frequently exceeding 10 percent of standard length; always larger than snout length, which never attains 10 percent of standard length (usually less than 9 percent). First dorsal spine never exceeding 12 percent of standard length (usually about 10.5 percent); only consistently exceeding fourth from last, third from last, and penultimate dorsal spines; always exceeded by tenth dorsal spine. Length of shortest pelvic ray contained $1\frac{4}{5}$ to $2\frac{2}{3}$ times in longest. Interspace between nuchal cirri bases contained $1\frac{1}{2}$ to $2\frac{1}{2}$ times in a single base. Maxillary length 7.9 to 9.3 percent of standard length. Largest specimen 50.3 mm.

Scales present on midline before dorsal, on prepectoral area, and on breast.

There are two preopercular canals extending onto the opercle, the more ventral of which is the longest and extends 1/5 to 2/5 the distance across the opercle.

Color pattern is variable and differences between the two subspecies are nebulous. Usually the same markings are present in both subspecies, but are distinct in *mexicanus* and fuzzily blotched in *margaritae.*

Coloration is here described from specimens from the type locality of *mexicanus.*

The major differences in the coloration between the sexes are to be found in the color pattern on the body. Males are more uniformly colored and the nature of the bars on the body are more readily recognized. In females there is extensive spotting on the sides and the bars are broken up, and are thus not clearly recognizable.

The dorsal, anal, and caudal fins are lightly and delicately spotted. Occasionally the anal is dusky. Some males lack spotting on the dorsal and caudal. There is a subbasal, dusky streak on the spinous dorsal. The pelvics and pectorals are clear, except for a few spots at the bases of the pectoral rays. Infrequently, there is a spot at the base of each pelvic fin.

The venter is uniformly light, and the ventral portion of the head is finely spotted or lined with dark on a light ground color. The sides of the head are variously lined with dark; the most prominent marking is a line which extends ventrally from each orbit onto the branchiostegal membranes.

Relationship. This species is most closely related to the Atlantic *M. macropus* by the nature of its pectoral count and scalation of the breast and prepectoral area. It differs from that species most prominently in dentition, spine lengths, and in the absence of fleshy pads on the pelvics of mature males. It differs from all species of *Malacoctenus*, except *M. boehlkei* and *M. erdmani*, in having a higher pectoral count; it differs from these latter two species most prominently in lacking small teeth behind the large outer row in each jaw.

MALACOCTENUS MARGARITAE MARGARITAE (Fowler)

(Plate III, Fig. 4)

Acteis margaritae Fowler, 1944: 285.
Acteis sp. Hubbs, 1952: 105.

This subspecies is separated from *M. m. mexicanus* under the account; for that subspecies.

Hubbs (1952) overlooked Fowler's description in reporting an undescribed species of *Acteis* from the Panamanian province.

Material. Forty specimens were examined. Nine from Piedra Blanca Bay, Costa Rica: SU 49681; 7 from Port Parker, Costa Rica: SU 49680; 1 from Bahia Honda, Panama: SU 49682; 23 from the Perlas Islands, Panama: ANSP 70050–59, 70047 (holotype of *A. margaritae*); UCLA W53–292, W53–283.

MALACOCTENUS MARGARITAE MEXICANUS, New Subspecies

(Plate III, Fig. 5)

Malacoctenus m. mexicanus differs from *M. m. margaritae* in having a larger average number of symphysial pores, a smaller average number of scales in a longitudinal series between the anterior lateral line and the dorsal contour (Table 2), and in having the

TABLE 2

Frequency Distributions of Symphysial Pores and Number of Scales in a Longitudinal Series between the Anterior Lateral Line and Dorsal Contour in Subspecies of *Malacoctenus margaritae*

	Pores				Scales		
	1	2	3	4	3	4	5
margaritae	4	13	6	6	19	5	....
mexicanus	67	6	4	1	....	67	4

length of the shortest pelvic ray contained in the longest usually more than 2¼ times (usually less than 2⅛ times in *margaritae*).

The subspecies are allopatric, separated by approximately seven hundred miles of coast line from which no clinids are known. *Malacoctenus m. margaritae* is known only from those areas south of the Gulf of Fonseca, and *M. m. mexicanus* only from those areas north of the Gulf of Tehuantepec.

Holotype. USNM 174956, an adult male, 46.6 mm. in standard length, from the south side of Bahia Santa Inez, Baja California, Gulf of California, Mexico (UCLA field number W53–86). Collected by Dr. Boyd W. Walker and party, April 26, 1953.

Paratypes. One hundred eighty-three specimens. Eighty-five parachronotopotypes: USNM 174959; 94 from the Islas Venados: BMNH 1957.5.1.51–76, CNHM 61905, UCLA W53–91, W53–89; 1 from Inez Island: SU 49683; 1 from Bahia Conception, Baja California, Gulf of California: UCLA W53–97; 1 from Punta de las Cuevas, Sonora, Gulf of California: UCLA W52–51; 1 from Acapulco, Guerrero: SU 49684.

Named *mexicanus* because it is found only on the coast of Mexico.

MALACOCTENUS GILLI (Steindachner)

(Plate IV, Figs. 1 and 2)

Clinus gilli Steindachner, 1867: 352.
Labrisomus biguttatus Cope, 1871: 473.
Myxodes lugubris Poey, 1875: 173; Jordan 1887a: 599; Lee, 1889: 669.
Myxodes varius Poey, 1875: 174; Jordan, 1887a: 599; Lee, 1889: 669*.
Clinus bimaculatus Steindachner, 1876: 228; Metzelaar, 1919: 153; Metzelaar, 1922: 135.
Labrisomus gilli, Jordan, 1887a: 599.
Malacoctenus varius, Jordan and Evermann, 1896: 467; Jordan and Evermann, 1898: 2357; Bean, 1905: 319*; Rosen, 1911: 67; Jordan, Evermann, and Clark, 1930: 459.
Malacoctenus lugubris, Jordan and Evermann, 1896: 467; Jordan and Evermann, 1898: 2357; Bean, 1905: 319; Jordan, Evermann, and Clark, 1930: 460.
Malacoctenus gilli, Jordan and Evermann, 1896: 467; Jordan and Evermann, 1898: 2358; Fowler, 1920; 149*; Jordan, Evermann, and Clark, 1930; 460; Longley, 1933: 294; Butsch, 1930: 30*; Fowler, 1944: 472*.
Malacoctenus bimaculatus, Jordan and Evermann, 1896: 468; Jordan and Evermann, 1898: 2358; Rosen, 1911: 67*; Jordan, Evermann, and Clark, 1930: 460; Herre, 1942: 17 (in part); Kanazawa, 1952: 91.

PLATE IV

Arranged Top to Bottom

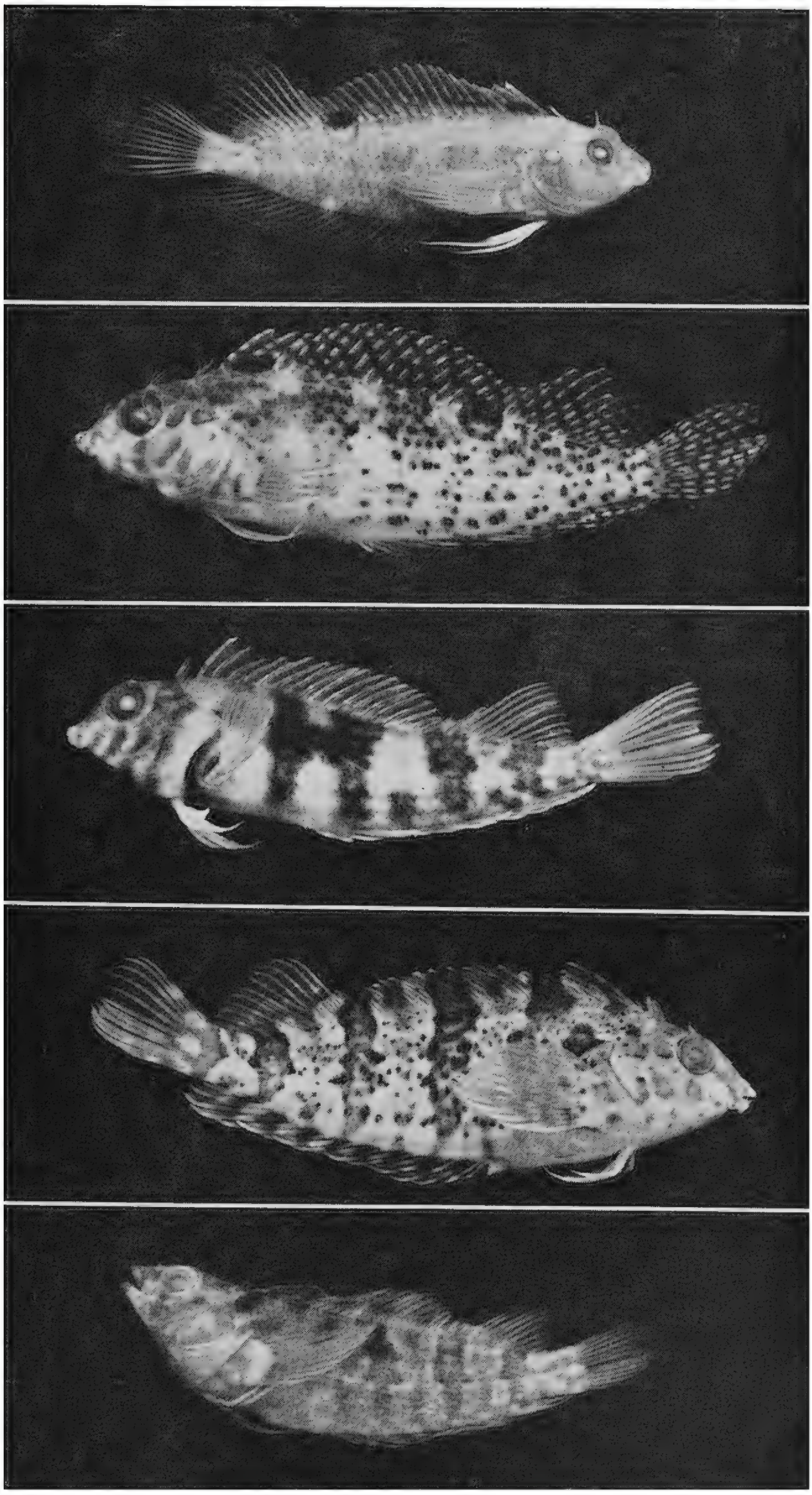
FIG. 1. *Malacoctenus gilli*, ANSP 74717, an adult male, 49 mm. in standard length, from Silver Cay, Bahamas.

FIG. 2. *Malacoctenus gilli*, UM 889, an adult female, 38.5 mm. in standard length, from Nicholstown, Andros Island, Bahamas.

FIG. 3. *Malacoctenus aurolineatus*, ANSP 74730, an adult male, 40 mm. in standard length, from Sandy Cay, Bahamas.

FIG. 4. *Malacoctenus versicolor*, UM 852, an adult female, 56.5 mm. in standard length, from Cay Sal Bank, Bahamas.

FIG. 5. *Malacoctenus africanus*, UZMK P76932, a young male, 32.3 mm. in standard length, from Dakar, Senegal.



Malacoctenus biguttatus, Jordan and Evermann, 1896: 468; Jordan and Evermann, 1898: 2360; Bean, 1905: 319; Rosen, 1911: 67*; Fowler, 1920: 151; Beebe and Tee Van, 1928: 229; Jordan, Evermann, and Clark, 1930: 460; Longley, 1932: 300; Schmitt and Schultz, 1940: 9; Fowler, 1944: 472; Fowler, 1952: 105; Fowler, 1953: 69.

Malacoctenus puertoricensis Evermann and Marsh, 1900: 358; Evermann and Marsh, 1900B: 309; Jordan and Evermann, 1900: 3189; Fowler, 1928: 467; Jordan, Evermann, and Clark, 1930: 460; Nichols, 1930: 376; Fowler, 1942C: 12* (spelled *portoricensis*); Fowler, 1944: 472 (spelled *portoricensis*); Smith, 1957: 14.

Labrisomus albipes Fowler, 1944: 117.

Description. Fin rays: dorsal XVIII, 10; XIX, 10 or 11; XX, 9 to 11; or XXI, 9 or 10 (XX, 10 in more than 55 percent of specimens from any locality; usually more than 60 percent); anal II, 17 to 21 (18 to 20); pectorals 13 to 16 (14). Lateral line 42 to 47. Gill-rakers 9 to 12. Symphysial pores 1 or 2 (1).

Head 26 to 30 percent of standard length in specimens over 24 mm. Bony orbital diameter larger than snout in specimens under 32 mm.; usually smaller than snout in specimens over 40 mm.; frequently exceeding 10 percent of standard length in the smaller specimens; rarely reaching 10 percent in the larger specimens. First dorsal spine always more than 10 percent of standard length (usually more than 11 percent); always exceeding third, fourth, and last four dorsal spines; always exceeded by 10th dorsal spine, which is rarely less than 12 percent of standard length. Length of shortest pelvic ray contained 1 9/10 to 2 7/10 times in longest. Interspace between nuchal cirri bases contained ½ to 1½ times in a single base. Maxillary length 8.8 to 10.7 percent of standard length. Largest specimen 58 mm.

Scales never present on midline before dorsal or on prepectoral area; usually present on breast.

There are two preopercular canals which scarcely encroach on the opercle.

Mature males have a large fleshy pad enveloping the innermost ray of each pelvic fin.

There is considerable dimorphism of coloration between the sexes. In males the anal and caudal are uniformly light dusky. The dorsal is marked regularly with dusky and has a dark blotch basally on the membranes of the anterior three spines, and another of slightly less intensity extending from basally on the membranes of the last four dorsal spines to the back. The pectorals are clear, except for a dusky crescent at the bases of the rays. The pelvic is perfectly clear. The body is uniformly dark dusky with faint indications of about six bands. The prepectoral area is usually covered by a reticulation of dark lines, as is occasionally the underside of the head. The venter and head are uniformly dark.

In females the dorsal, anal, and caudal fins are densely spotted. There are two blotches on the dorsal similar to those in the male. The pectorals are clear, except for a few faint spots at the bases of the rays. The pelvics are unmarked. The bars on the body appear as areas slightly darker than the ground color of the body. Their margins are outlined by spots of a similar size to those on the fins. The venter is usually lighter in color than the sides of the body. The prepectoral area is spotted, or, rarely, shows the reticular pattern found in males. The underside of the head is light or barred with dark and light stripes, at least one of which extends to beneath the middle of both orbits. There are two spots behind the eye; one each on the dorsal margin of the preopercle and opercle.

Young males are similar to females in color pattern. Color pattern is recognizable in specimens of 12 mm.

There is a tendency for prominent markings to fade in specimens which have been preserved for a long period of time.

Discussion. There is some indication of a cline in dorsal and anal counts (Table 3); the Bahamas representing one extreme and the more eastern Antilles, the other.

TABLE 3

Frequency Distributions of Total Anal and Total Dorsal Elements in *Malacoctenus gilli*

	Dorsal					Anal			
Elements	19	20	21	22	23	28	29	30	31
Bahamas	....	.. .	34	33	3	....	2	43	30
Cuba	....	4	29	3	....	....	3	31	4
Puerto Rico	1	8	70	10	....	....	13	70	7
Virgin Islands	....	....	12	8	....	1	1	15	3
Barbados	....	6	27	....	....	....	10	24	....
Tobago	....	....	4	....	....	....	....	4	....
Curaçao	....	....	2	....	....	....	....	2	....
Courtown Cay	....	....	1	....	....	....	1	....	.. .
Old Providence Island	....	....	1	....	....	....	....	1	.. .
Honduras	....	....	....	1	....	....	.. .	....	1
British Honduras	....	1	.. .	....	....	.. .	1	....	....
Cayman Islands	....	....	1	....	....	....	....	1	....
Tampico, Mexico	....	....	1	.. .	....	....	....	1	....
Bermuda	....	....	....	1	....	....	....	1	....

All nominal type material, except that of *Clinus gilli* and *C. bimaculatus*, was examined. A photograph of one of the two syntypes of *C. gilli* was kindly given to me by Dr. Kähsbauer of the Vienna Museum, and has been deposited in the U.S. National Museum. The color of this specimen is almost completely lost. As I have been unable to examine either specimen, designation of a lectotype cannot be made at the present time.

The description of *Labrisomus albipes* Fowler is based on a young male of *M. gilli*.

Relationship. Malacoctenus gilli differs from all other *Malacoctenus* in the nature of its color pattern. It is similar to *M. erdmani*, *M. macropus*, and *M. aurolineatus* in that mature males have the median pelvic rays enveloped in large fleshy pads. In addition to coloration, it differs from the first two in the nature of its dentition and by its lower pectoral count; and from the latter in never having a hook on the cleithrum, in the nature of its scalation, and in the nature of the preopercular pores extending onto the opercle.

Material. Two hundred eighy-one specimens were examined. Eighty-eight from the Bahamas: ANSP 7767, 10590 (holotype of *L. biguttatus*), 72600–05, 74667–71, 74717–18 (including one stained), MCZ 34168, UM 854, 889, USNM 38381; 39 from Cuba: USNM 37538–39 (holotypes of *M. varius* and *M. lugubris*, respectively), 82542, 82587–88; 86 from Puerto Rico: SU 8656, UMMZ 171161, 171166, 171170, 171174, 171178, 171182, 171186, 171191, 171203, 171209–10, 171216, 171221–23, 171227–28, 171230, 171234, 171236, USNM 49371 (holotype of *M. puertoricensis*), 50180, 125974, 128802, 147634; 20 from the Virgin Islands: UZMK 82, 3–19, P76257, ANSP 73298; 34 from Barbados: ANSP 74672–74, SU 32035; 1 from the Grenadines: AMNH 17385; 4 from Tobago: BMNH 1931.125.361–364; 2 from Curaçao: USNM 38534, 92807; 1 from Courtown Cay (holotype of *L. albipes*): ANSP 69994; 1 from Old Providence Island: USNM 107112; 1 from Honduras: CNHM 39843; 1 from British Honduras: CNHM 39822; 1 from the Cayman Islands: BMNH 1939.5.12.178A; 1 from Tampico, Mexico: BMNH 1908.7.6.24.

MALACOCTENUS AUROLINEATUS Smith

(Plate IV, Fig. 3)

Malacoctenus biguttatus, Fowler, 1950: 89 (not of Cope).
Malacoctenus aurolineatus Smith, 1957: 2.

Description. Fin rays: dorsal XVIII, 10 or 11; XIX, 10 to 12; XX, 10 to 12; or XXI, 10 or 11 (XIX or XX, 11 in 80 percent of specimens); anal II, 17 to 21 (19 or 20); pectorals 13 to 15 (14). Lateral line 42 to 55 (48 to 53). Gill-rakers 10 to 12. Symphysial pores 1 to 4 (1 or 3).

Head 24.4 to 30.4 percent of standard length in specimens over 26 mm. Bony orbital diameter 7.5 to 10.4 percent of standard length; only rarely exceeding snout length, which is 7.6 to 11.3 percent of standard length in specimens over 26 mm. (either of these measurements usually less than 10 percent of standard length). First dorsal spine rarely less than 10 percent of standard length; never exceeded by second, third, or last four dorsal spines which rarely attain 10 percent of standard length; always exceeded by tenth dorsal spine which is rarely less than 12 percent of standard length; sometimes exceeded by fourth and fifth dorsal spines. Length of shortest pelvic ray contained 1⅔ to 1 9/10 times in longest. Interspace between bases of nuchal cirri contained 3 to 7 times in a single base. Maxillary length 8.1 to 10.6 percent of standard length. Largest specimen 46.5 mm.

Scales never present on midline before dorsal, prepectoral area, or breast.

There are three preopercular canals extending onto the opercle; the middle one, which is the longest, extends ⅓ to ½ the distance across the opercle.

A hook is usually present on the anterior margin of the cleithrum in adults.

Mature males have a large fleshy pad enveloping the innermost ray on each pelvic fin.

There is a difference in coloration between the sexes. Mature males have the color pattern more darkly emphasized than do most females. Infrequently, the females will have a light delicate spotting on the dorsal, whereas the males never do.

All the fins are clear, except for a light dusky streak which extends subbasally along the spinous dorsal.

There are six rectangular bands on the body separated by lighter interspaces, the last three of which contain subquadrate splotches below the midline of the body. The middle interspace is noticeably the largest. The mid-portions of the anterior three bands may be strikingly darker than the others, and they are occasionally fused, forming an elongate humeral splotch. There are two dark lines in the prepectoral areas, the anterior of which may extend across the prepelvic area, joining the two sides. The venter is uniformly light. The ventral portions of the head may be uniformly dusky or lightly barred with dark and light. In some individuals, usually males, this barring may be well developed. The head is variously marked with dusky, and there is usually a dark line below the eye which is continuous with one of the bars below the head.

Specimens of 13 mm. show indications of adult coloration, and specimens of 15 mm. have the adult color pattern in all particulars.

Discussion. Specimens from Puerto Rico have modally 21 total anal and 30 total dorsal elements; specimens from the Bahamas, Cuba, and Campeche Banks have modally 22 total anal and 31 total dorsal elements.

Relationship. Malacoctenus aurolineatus appears to be quite different from all other *Malacoctenus*, particularly in the nature of its color pattern. In having the inner pelvic

rays enveloped by fleshy pads in mature males, it resembles *M. macropus*, *M. erdmani*, and *M. gilli*. In addition to color pattern, it differs from the first two in dentition and pectoral count, and from the latter in the nature of scalation, the preopercular canals on the opercle, the nuchal cirri, and the number of times the length of the shortest pelvic ray is contained in the longest.

Material. One hundred seventy-five specimens were examined. One from Tortugas, Florida: USNM 114715; 74 from the Bahamas: ANSP 72589, 74519–29, 74692–94 (including one stained), 74730; 43 from Cuba: USNM 82534–35, 114708, 114710, 114759; 10 from Puerto Rico (paratypes): UMMZ 171162–63, 171185, 171190, 171214; 1 from the Virgin Islands: UZMK P76991; 1 from Tobago: BMNH 1922.6.22. 109; 1 from St. Andrews Island: ANSP 72682; 42 from Campeche Banks, Mexico: CNHM 46652.

MALACOCTENUS VERSICOLOR (Poey)

(Plate IV, Fig. 4)

Myxodes versicolor Poey, 1875: 173; Jordan, 1887: 599.

Ma'acoctenus versicolor, Jordan and Evermann, 1896: 468; Jordan and Evermann, 1898: 2359; Jordan, Evermann, and Clark, 1930: 460; Smith, 1957: 14.

Malacoctenus delalandi, Herre, 1942: 17 (not of Valenciennes).

Description. Fin rays: dorsal XVIII, 11 or 12 (12 in 25 out of 27 specimens); anal II, 18 or 19; pectorals 13 or 14 (14). Lateral line 59 to 64. Gill-rakers 11 to 13 (12 or 13). Symphysial pores 1 to 5.

Head 26.2 to 27.8 percent of standard length in specimens over 36 mm. Bony orbital diameter 7.8 to 8.9 percent of standard length in specimens over 36 mm.; never much larger (usually less) than snout length. First dorsal spine 11.3 to 15.8 percent of standard length (rarely less than 12 percent); always exceeding all other dorsal spines, except the second which occasionally equals the first. Length of shortest pelvic ray contained 1⅕ to 1½ times in longest. Interspace between nuchal cirri bases contained 1⅓ to 6 times in a single base (usually less than 2½ times). Maxillary length 8.6 to 9.7 percent of standard length. Largest specimen 64 mm.

Scales not present on midline before dorsal, or on prepectoral area of specimens under 30 mm. Scales usually present on breast.

There are three preopercular canals extending onto the opercle. The middle canal is the longest and extends from 1/5 to 3/5 the distance across the opercle.

Female coloration differs from that of males in the presence of scattered small, dark spots in the interspaces between the bands on the body.

There are five or six bands on the body, the anterior four of which extend undiminished onto the spinous dorsal. The interspaces between the bands are dusky over a light ground color. The venter may be uniformly light or with a few heavy markings. The prepelvic region and ventral portions of the head are light or spotted. Three dark "spokes" with lighter interspaces extend from the eye: one anteroventrally, one medianventrally, and one posteriorly. The opercle is variably blotched.

The interspaces between the bands on the spinous dorsal are clear or dusky. The soft dorsal is variably dark spotted. The caudal and anal are barred. The pelvics are uniformly light, except for the median ray on each, which is uniformly dark. The pectorals are dusky or spotted, with the darkest areas anteroventrally.

Discussion. The location of the holotype of *M. versicolor* is not known; however, Poey's designation and figure are sufficient for the establishment of the identity of this form. The designation of a neotype would serve no useful purpose.

Relationship. This species appears to be most closely related to *M. africanus*, as indicated by the nature of the coloration and lateral line scale count. It differs from that species in the nature of the dorsal formula and preopercular pores extending onto the opercle. When more specimens of *M. africanus* are available it may be found that these two species are conspecific.

Material. Twenty-eight specimens were examined. Four from the Bahamas: BMNH 1939.4.19.39, UM 852, 887; 1 from Cuba: USNM 114752; 2 from Puerto Rico UMMZ 171151, USNM 117435; 1 from the Virgin Islands: UZMK P76935; 15 from Barbados: ANSP 74477, SU 37289; 5 from Tobago: BMNH 1920.12.22.184–186, 1924.7.22.77.

MALACOCTENUS AFRICANUS Cadenat

(Plate IV, Fig. 5)

Malacoctenus africanus Cadenat, 1950: 271.

Description. Fin rays: dorsal XX, 10; anal II, 19; pectorals 14. Lateral line 60. Gill-rakers 11. Symphysial pores 2.

Head 30.6 percent of standard length. Bony orbital diameter 9.3 percent of standard length. Snout length 9.9 percent of standard length. First dorsal spine 13.6 percent of standard length, exceeding all others. Length of shortest pelvic ray contained 1⅔ times in longest. Interspace between nuchal cirri bases contained 1½ times in a single base. Maxillary length 11.1 percent of standard length. Only one specimen examined 32.3 mm. (maximum length recorded in original description 73.5 mm.).

Scales not present on midline before dorsal; present on prepectoral area and breast.

None of the preopercular pores can be considered as extending onto the opercle.

The specimen examined is a male. There are six bands on the body, the anterior four of which extend undiminished onto the spinous dorsal. Between the second, third, and fourth bands from the posterior, are lighter bands. The ground color of the interspaces is dusky. The head and venter are dusky. There are four faint "spokes" extending from the orbit: one anteroventrally, one medianventrally, one posteriorly, and one dorsoposteriorly.

The interspaces between the bands on the dorsal fin are dusky, as are the entire soft dorsal, caudal, pelvic, and pectorals (except for a blotch at the bases of the rays).

Discussion. In his paper, Cadenat (1950) gave a crude drawing which he labeled: *Malacoctenus africanus* Cadenat. In the text, under the heading "*Malacoctenus,*" he makes the statements: "*Ce genre de Blenniidae à écailles est nouveau por la côte occidental d'Afrique. Un espèce, qui sera décrite sous le nom de M. africanus. . . .*" Obviously, Cadenat did not intend to describe this species at that time. This is further evidenced by the fact that he designated no type material. He did, however, distinguish the form from the other clinid (*L. nuchippinnis*) in the Dakar area. All attempts to contact Dr. Cadenat have failed to elicit response, and I have been unable to examine any of his material. Nevertheless, the figure, the name, and the differentiation given in his paper are sufficient to constitute species description; and so the name must stand. The type becomes, then, the figure (No. 211, page 270). From this figure I am able to count twenty dorsal spines and possibly ten rays; the same number as in the single specimen I have examined.

Relationship. This species appears to be most closely related to the western Atlantic *M. versicolor*, and may ultimately prove to be conspecific with it. It differs from *M. versicolor* in the dorsal formula and in the nature of the preopercular pores extending onto the opercle.

Material. One specimen was examined from Dakar, Senegal: UZMK P76932.

MALACOCTENUS GIGAS, New Species

(Plate V, Figs. 1 and 2)

Malacoctenus delalandi, Seale, 1940: 38 (in part; not of Valenciennes).

Description. Fin rays: dorsal XIX, 12; XX, 11 to 14; XXI, 10 to 13; XXII, 11 to 13; or XXIII, 13 (XXI, 12 in 70 percent of specimens); anal II, 20 to 24 (22 or 23); pectorals 13 to 15 (14). Lateral line 53 to 65 (56 to 62). Gill-rakers 9 to 12 (10 or 11). Symphysial pores 1 to 3 (1 or 2).

Head 23.4 to 31.0 percent of standard length in specimens over 22 mm. (less than 28 percent in specimens over 45 mm.). Bony orbital diameter always shorter than snout and less than 8.5 percent of standard length in specimens over 60 mm.; always larger than snout and more than 8.5 percent of standard length in specimens under 42 mm.; rarely attaining 10 percent of standard length in specimens over 35 mm. Snout always less than 10 percent of standard length. In specimens from Guaymas and environs the first dorsal spine usually exceeds 13 percent of the standard length and all other dorsal spines. In specimens from other localities the first dorsal spine is frequently between 10 and 13 percent of the standard length; decreasing in proportional size with increasing standard length (always more than 11 percent of standard length in specimens under 45 mm. and usually less than 11 percent in specimens over 60 mm.); it always exceeds the third, fourth, fifth, and last four dorsal spines (frequently exceeds all dorsal spines in specimens under 40 mm.); it is always exceeded by the tenth dorsal spine in specimens over 60 mm.; and is sometimes exceeded by the second dorsal spine in specimens over 60 mm. Length of shortest pelvic ray contained 1⅓ to 1¾ times in longest. Interspace between nuchal cirri bases contained ½ to 1 time in a single base. Maxillary length 6.9 to 10.8 percent of standard length (usually less than 10 percent). Largest specimen 96.5 mm.

Scales present or not on midline before dorsal; present on prepectoral area of all specimens over 32 mm.; present on breast of all specimens over 46 mm.

There are two to four preopercular canals extending onto the opercle, the longest of which extends less than one-half the distance across the opercle (usually less than one-quarter the distance).

Coloration differs between the sexes. Males have the dorsal, anal, and caudal uniformily dusky. The membranes of the anterior three dorsal spines are the darkest, and there is frequently a dark stripe subbasally on the spinous dorsal. The pectorals are clear with a dark, crescent mark extending over the bases of the rays. The pelvics are dusky with the innermost ray the darkest. The body has five irregular bands which are darker above the midline of the body; the anterior three bands do not extend ventrally as far as the anal base. The interspaces between the bands are uniformly dusky, darker above, and sometimes diffusely splotched ventrally. The venter is uniformly light and the ventral portion of the head is diffusely dusky. The sides of the head are variable; darker above and usually with either dark or light spots on the lower third.

Females have the dorsal, anal, and caudal spotted. The pectorals, pelvics, and bands

on the body are like those of the male. The interspaces between the bands are darker above and contain a diffuse reticular pattern below. The venter is similar to that of the male. The ventral side of the head is diffusely mottled as are the sides of the head. Frequently the entire body and head are suffusd with light specks.

Specimens of about 18 mm. show indications of adult coloration.

The following description of life coloration is taken from the field notes of Dr. Clark Hubbs (field number Q48–3):

Ground color olive-green above. Two bluish stripes one scale width just above posterior lateral line. Color orange-brown below with bluish-whitish blotches covering about five scales. Abdomen white. Head olive-brown with bluish spots below eye and on cheek. Lower part of head olive-yellow. Membranes of spinous dorsal olive-green with four irregular rows of blotches on spines. Lower one blackish, upper ones orange-brown. Soft dorsal same, has seven orangish blotches and upper membranes whitish. Caudal membranes colorless; rays have seven alternate rows of orangish and yellowish stripes. Anal membranes orange-brown; rays with white, orange-brown, and yellow stripes; orange-brown from membranes then cover rays. Anterior tips whitish. Pectoral membranes colorless, rays almost so; colored at base with a blackish stripe. Above that three alternate stripes of yellow. Spinous dorsal where fin indents, fewer rows of blotches; orange-brown. Outer half of ray orange-brown. Pelvic orange-brown darker at tip.

Discussion. This species, which attains the largest size of all the species of *Malacoctenus*, is restricted to the waters of the Gulf of California. Frequency distributions of total anal and dorsal elements (Table 4) indicate the possible presence of a cline when localities are listed north to south; a break possibly occurs at that latitude passing through Guaymas. Comparisons of specimens from opposite coasts of the Gulf show no significant differences, except for the longer first dorsal spines found in specimens

TABLE 4

Frequency Distributions of Total Anal and Total Dorsal Elements in *Malacoctenus gigas*, Arranged Geographically from North to South

	Anal					Dorsal					
	22	23	24	25	26	31	32	33	34	35	36
Vicinity of Punta Peñasco and Punta Cholla	21	65	353	76	1	3	31	371	109	....	2
Vicinity of San Felipe	....	....	....	2	....	....	....	....	1	1	....
Vicinity of Punta Diggs	....	1	11	1	....	....	....	12	1	....	....
Isla San Luis	....	....	2	....	....	....	....	1	1	....	....
Isla Mejia	....	....	1	....	....	....	....	1	....	....	....
Isla Angel de la Guarda	....	4	6	....	....	....	1	8	1	....	....
Northern Isla Tiburon	....	5	41	2	....	....	5	38	6	....	....
Bahia los Angeles	....	2	13	1	....	....	....	12	4	....	....
Isla Partida	....	1	....	....	....	....	1	....	....	....	....
Southern Isla Tiburon	....	....	9	....	....	....	....	9	....	....	....
Bahia San Francisquito	....	4	14	....	....	....	2	15	1	....	....
Guaymas and vicinity	....	27	87	....	....	....	9	102	3	....	....
Santa Inez and vicinity	....	15	38	....	....	....	8	43	3	....	....
Isla Espiritu Santo	....	11	17	2	....	1	2	25	2	....	....

PLATE V

Arranged Top to Bottom

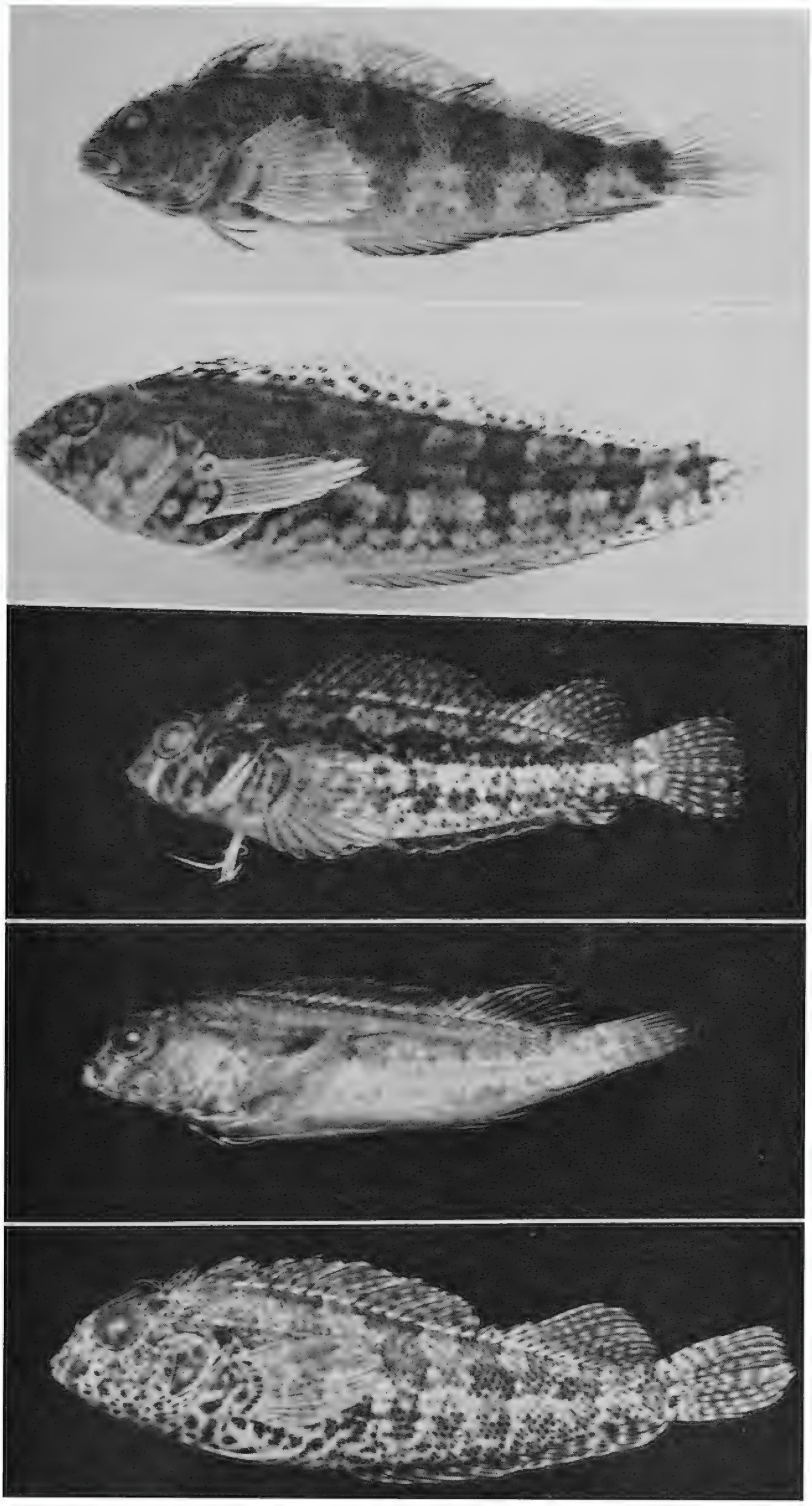
FIG. 1. *Malacoctenus gigas*, SU 49648, an adult male, 75 mm. in standard length, from Bahia San Francisquito, Baja California, Mexico.

FIG. 2. *Malacoctenus gigas*, SU 49618, an adult female, 80.5 mm. in standard length, from Punta Cholla, Sonora, Mexico.

FIG. 3. *Malacoctenus delalandei*, SU 17870, an adult female, 41.5 mm. in standard lenth, from Ustup Island, Cape San Blas, Panama.

FIG. 4. *Malacoctenus afuerae afuerae*, USNM 128214, an adult female, 46 mm. in standard length, from Lobos de Afuera Bay, Peru.

FIG. 5. *Malacoctenus afuerae multipunctatus*, CNHM 61900, an adult female, 48 mm. in standard length, from Bahia Santa Inez, Baja California, Mexico.



from the immediate vicinity of Guaymas as compared to first dorsal spine lengths of specimens from other localities.

Relationship. Malacoctenus gigas appears to be most closely related to a group of species comprising also *M. afuerae* in the Pacific, and *M. delalandei* in the Atlantic. It can be distinguished from the former and the other Pacific species by the characters given in the key. It differs from all the Atlantic species, except *M. boehlkei*, in its typically high anal and dorsal formulae. It differs from all but *M. gilli*, *M. erdmani*, and *M. boehlkei* in the number of times the interspace between the nuchal cirri bases is contained in a single nuchal cirrus base. It differs from the first of these in its larger number of lateral line scales, and from the latter two in the nature of its dentition and lower pectoral count.

Holotype. SU 49617, an adult male, 78 mm. in standard length, from 250 yards south of the tip of Punta Cholla, Sonora, Mexico (six miles north of Punta Peñasco). Collected by Clark Hubbs and Janet Haig, March 19, 1948.

Paratypes. Eight hundred forty-six specimens. Five hundred thirteen from the vicinity of Punta Peñasco and Punta Cholla, Sonoro: SU 47183–84, 49618 (parachronotopotypes), 49624–31, 49534–42. UZMK 76956; 2 from the vicinity of San Felipe, Baja California: SU 49623. UCLA W54–193; 13 from the vicinity of Punta Diggs, Baja California: UCLA W52–69, W52–192A, W54–194; 2 from Isla San Luis: UCLA W52–74; 1 from Isla Mejia: SU 49646; 10 from Isla Angel de la Guarda: UCLA W54–20; 58 from Isla Tiburon: CNHM 61903. SU 17875. 49619. UCLA W56–27; 16 from just south of Bahia Los Angeles, Baja California: TNHC 2973; 1 fom Isla Partida: SU 49647; 3 from Bahia San Pedro, Sonora: SU 49649; 18 from Bahia San Francisquito, Baja California: SU 49648; 115 from Guaymas and vicinity, Sonora: CAS 20721–22, SU 16483, 16537, 16644–45. 16655, 19180, 49643–45, 49622, UCLA W52–51; 54 from the vicinity of Santa Inez. Baja California: BMNH 1957.5.1.205–236. SU 49620–21, 49650, UCLA W53–86, USNM 174961; 30 from Isla Espiritu Santo: CAS 6041.

Named *gigas* because of its being the largest member of its genus.

MALACOCTENUS DELALANDEI (Valenciennes)

(Plate V, Fig. 3)

Clinus delalandii Valenciennes (in Cuvier and Valenciennes), 1836: 379; Gűnther, 1861: 264 (in part).

Labrisomus delalandii, Swainson, 1839: 277.

Clinus delalandi, Műller, 1864: 632 (in part); Gűnther, 1868: 389 (in part).

Malacoctenus delalandi, Gill, 1860: 103; Jordan and Evermann, 1896: 468 (in part); Gilbert, 1900: 179; Evermann and Marsh, 1900: 310; Jordan, Evermann, and Clark, 1930: 459 (in part); Nichols, 1930: 376; Fowler, 1942A: 178.

Labrisomus delalandi, Jordan, 1887: 599.

Malacoctenus delalandii, Meek and Hildebrand, 1928: 938; Fowler, 1944: 472; Schultz, 1949: 179.

Description. Fin rays: dorsal XIX, 9 to 11; XX, 9 to 11; or XXI, 9 (XX, 10 in 75 percent of specimens); anal II, 17 to 20 (19); pectorals 13 to 15 (14). Lateral line 48 to 54. Gill-rakers 10 to 12. Symphysial pores 1 to 6 (3 or 4).

Head 26.5 to 29.2 percent of standard length in specimens over 25 mm. Bony orbital diameter 8.3 to 11.2 percent of standard length; always larger than snout length, which does not exceed 10 percent of standard length. First dorsal spine 10 to 13 percent of

standard length; only consistently exceeding third, fourth, fourth from last, third from last, and penultimate dorsal spines; usually exceeded by tenth dorsal spine. Length of shortest pelvic ray contained 1⅓ to 2 times in longest. Interspace between nuchal cirri bases contained 1½ to 8 times in a single base (usually 2 to 4 times). Maxillary length 8.2 to 9.8 percent of standard length. Largest specimen 55.8 mm.

Scales not present on midline before dorsal or on prepectoral area. Breast usually scaled in adult males; mostly naked in females. The breast scales become fleshy in mature males.

There are two or three preopercular canals extending onto the opercle, the more ventral is the longest, extending two-fifths to one-half the distance across the opercle.

Coloration depends on sex and geographic distribution. Females have the dorsal, anal, and caudal fins densely spotted; body pattern is overlain by numerous irregular patches of dusky spots. In contrast to this, the fins of males are uniformly colored, as is the body. Both sexes have the membranes of the anterior three or four dorsal spines more heavily pigmented than any of the others, and a dusky area running subbasally the length of the spinous dorsal. There is a dark, crescent mark at the base of the pectoral rays in all specimens, otherwise the pectorals and pelvics are unmarked.

The six irregular bands on the body are usually discernible in females, but rarely so in males. All specimens from Brazil, Panama, Venezuela, and Tobago have a well developed dark blotch covering most of the opercle. Only a few specimens from Guatemala and neither specimen from Puerto Rico showed indications of this blotch. The ventral portions of the body and head are uniformly dusky in males, but the ventral portion of the head is either barred with light and dark or spotted in females. The body is usually abruptly lighter below the midline. Four dark "spokes" with lighter interspaces extend from the eye: one anteroventrally, one ventrally (the most distinct), one posteriorly, and one dorsoposteriorly. Specimens 16 mm. long show indications of adult coloration, though the fins are variably spotted at this stage.

Discussion. This species was named for its collector, Delalande. It is therefore necessary to emend Valenciennes' name *delalandii* to *delalandei* in accordance with the rules of nomenclature.

Relationship. This species appears to be most closely related to the Pacific *M. afuerae* and *M. gigas*. It differs from the former most notably in the nature of the preopercular canals on the opercle, the typical formula of the dorsal, and the color pattern; and from the latter in dorsal and anal formulae, coloration, and the number of times the interspace between the nuchal cirri bases is contained in a single base.

Material. One hundred nineteen specimens were examined. Thirty from Guatemala: UMMZ 144151; 2 from Puerto Rico: USNM 50179, 126125; 2 from Tobago: BMNH 1924.7.22.78–79; 11 from Natal, Brazil: CNHM 61893, SU 49584; 7 from Venezuela: USNM 123170–71; 67 from Panama: USNM 81893–97, 114751, CNHM 26001–15, 18547, SU 17870, UCLA W53–268.

MALACOCTENUS AFUERAE (Hildebrand)

(For synonymy see subspecies)

Description. Fin rays: dorsal XVIII, 11 or 12; XIX, 10 to 12; or XX, 9 to 11 (XIX, 11 in 62 percent of specimens); anal II, 18 to 20 (19); pectorals 13 to 15 (14). Lateral line 53 to 61 (53 to 56). Gill-rakers 11 to 15 (11 to 13). Symphysial pores 3 to 13 (4 to 8).

Head length 27 to 31.4 percent of standard length in specimens over 15.5 mm. Bony orbital diameter larger than snout in specimens under 38 mm.; either of these measurements usually less than 10 percent of standard length. First dorsal spine never attaining 11.5 percent of standard length (usually less than 10 percent); always exceeding second through fourth and fifth from last through penultimate dorsal spines; always exceeded by other dorsal spines, except last, which it sometimes exceeds. Length of shortest pelvic ray contained 1½ to 1⅔ times in longest. Interspace between nuchal cirri bases contained more than four times (sometimes bases meet) in a single base. Maxillary length 9.3 to 11.2 percent (usually less than 10.5 percent of standard length. Largest specimen 56.6 mm.

Scales are not present on the midline before the dorsal fin; sometimes present on the prepectoral area; present on the breast of males only, the scales becoming fleshy with maturity.

There are two or three preopercular canals extending onto the opercle, the longest of which extends one-half to three-quarters the distance across the opercle. When two canals are present the more ventral one is the longest; when three canals are present the middle one is the longest.

Coloration is discussed under the subspecies.

Relationship. This species appears most closely related to the Pacific *M. gigas* and the Atlantic *M. delalandei.* It can be distinguished from the former by characters given in the key, and from the latter in the nature of the preopercular canals on the opercle, by the typical formula of the dorsal, and in coloration.

MALACOCTENUS AFUERAE AFUERAE (Hildebrand)

(Plate V, Fig. 4)

Labrisomus afuerae Hildebrand, 1946: 400.
Malacotenus afuerae, Hubbs, 1952: 104.

This subspecies is separated from *M. a. multipunctatus* under the account for that subspecies.

Because of the poor, or juvenile, condition of those specimens examined, it is necessary to refer to the original description and figure for purposes of determining the color pattern. In none of the specimens examined, nor in Hildebrand's figure or account is there to be found indications of a profuse spotting of the venter or sides of the body. Despite the poor condition of the type material it is hardly considered possible that spotting as found in *M. m. multipunctatus* ever existed, except on the ventral surface of the head. Faint indications of the body bands are still discernible in the type material.

Material. Six specimens were examined. One from Port Parker, Costa Rica: SU 49595; 1 from Chame Point, Panama: USNM 81963; 1 from Manta, Ecuador: USNM 143030; 3 from Lobos de Afuera Bay, Peru: USNM 128213 (holotype of *L. afuerae*), 128214.

MALACOCTENUS AFUERAE MULTIPUNCTATUS, New Subspecies

(Plate V, Fig. 5)

Malacoctenus a. multipunctatus diffffers from *M. a. afuerae* in the nature of its dense, dark spotting, which in most young and all adults encompasses all of the ventral regions anterior to the anus and the sides of the body and head below the midline (in females and

some males, all of the body, head, and unpaired fins). Spots on the venter and breast of males may be obscured by the presence of fleshy scales. Though only six specimens of *M. a. afuerae* are known, none approximate the spotted condition of *M. a. multipunctatus*.

Frequently males are lighter and more uniform in color than females, especially above the midline of the body. Usually the spotting on males takes the form of a fine peppering rather than a polka-dotting as found in females.

The complex color pattern is best understood by reference to the photograph rather than by a written description.

The two subspecies are allopatric, separated by approximately seven hundred miles of coastline from which no clinids are known. *Malacoctenus a. afuerae* is known only from those areas south of the Gulf of Fonseca and *M. a. multipunctatus* only from those areas north of the Gulf of Tehuantepec.

Holotype. SU 49596, an adult male 43.8 mm. in standard length, from the southwest end of San Lucas Bay, Baja California, Mexico. Collected by J. Böhlke, D. Cohen, and J. Lindbergh, May 20, 1952 (Field number: 44-TP-1).

Paratypes. One hundred thirty-seven specimens from Mexico. One from one and one-half miles south of Punta Peñasco, Sonora: SU 49599; 2 from Bahia Agua Dulce, Isla Tiburon, Gulf of California: UCLA W56–26; 1 from the southwest corner of Isla Partida, Gulf of California: SU 49600; 2 from Punta de las Cuevas, Sonora: UCLA W50–37; 90 from Bahia Santa Inez, Baja California: CNHM 61900, USNM 174962; 2 from Bahia Coyote in Bahia Concepcion, Baja California: UCLA W53–97; 7 parachronotopotypes: SU 49597; 7 from Cape San Lucas, Baja California: SU 18933; 1 from Mazatlan, Sinaloa: UCLA W51–58; 19 from the Islas Venados: BMNH 1957.5.1.77–87, UCLA W51–20, W51–33, W51–54; 2 from Mazanillo, Colima: UMMZ 171893; 3 from Puerto Marques, Guerrero: SU 49598.

Named *multipunctatus* for the numerous spots which distinguish it from the other species of *Malacoctenus*.

MALACOCTENUS HUBBSI, New Species

(For synonymy see subspecies)

Description. Fin rays: dorsal XIX, 10 to 13; XX, 9 to 12; or XXI, 10 to 12 (XX, 11 in 75 percent of specimens of *M. h. hubbsi* and 59 percent of specimens of *M. h. polyporosus*); anal II, 18 to 23 (19 to 21; 20 in 78 percent of *M. h. hubbsi* and 53 percent of *M. h. polyporosus*); pectorals 13 to 15 (14). Lateral line 49 to 61 (Table 5). Gill-rakers 10 to 14 (11 or 12). Symphysial pores 1 to 10 (Table 6).

Head 26.0 to 30.8 percent of standard length in specimens over 22 mm. Bony orbital diameter smaller than snout in specimens over 45 mm.; larger than snout in specimens under 35 mm. Either of these two measurements usually less than 10 percent of standard length. First dorsal spine rarely less than 11 percent of standard length, decreasing in proportional size with increasing standard length (as much as 28 percent of standard length in specimens under 25 mm., though usually 13 to 15 percent in specimens up to 45 mm.); usually exceeding second through fifth and last four dorsal spines; frequently exceeded by second and tenth dorsal spines in specimens over 48 mm. Length of shortest pelvic ray contained 1½ to 2 times in longest. Interspace between nuchal cirri bases contained 1 to 3½ times in a single base. Maxillary length 8.6 to 10.2 percent of standard length (usually less than 9.8 percent). Largest specimen 79.5 mm.

TABLE 5

Frequency Distributions of Lateral Line Scales in *Malacoctenus hubbsi* (Arranged North to South for Each Heading)

	49	50	51	52	53	54	55	56	57	58	59	60	61
M. h. hubbsi													
Pacific Coast, Baja California													
Puerta Mala Arrima	....	....	....	1	10	25	28	10	7	1	....	....	....
Bahia Magdalena	....	....	1	3	11	28	29	19	9	5	2	....	1
Gulf Coast, Baja California[1]													
Isla Mejia	....	....	....	....	....	2	7	11	9	5	3	....	....
Isla Angel de la Guarda	....	....	....	....	....	....	6	9	7	8	2	1	1
Isla Partida	....	....	....	....	....	3	11	15	9	9	3	4	....
Bahia San Francisquito	....	....	....	....	6	20	36	32	12	9	....	1	....
Bahia San Carlos	....	....	....	....	2	11	22	15	6	3	....	....	....
Isla Santa Inez	....	....	....	....	....	....	1	....	....	1	....	....	....
Bahia Santa Inez	....	....	....	....	2	5	20	16	8	1	....	1	....
Isla Ildefonso	....	....	....	2	1	2	10	8	22	15	1	....	....
Isla Coronado	....	....	....	....	....	....	....	....	1	....	....	....	....
Isla Monserrate	....	....	....	....	....	2	3	1	2	....	....	....	....
Bahia Agua Verde	....	....	....	....	1	1	1	4	2	1	1	....	....
Isla Cerralvo	....	....	....	....	....	2	....	2	....	....	....	....	....
Bahia de los Muertos	....	....	....	....	1	3	2	....	1	1	....	....	....
Punta Frailes	....	....	....	....	....	....	4	1	1	....	....	....	....
San Lucas	....	....	....	....	....	2	....	....	....	....	....	....	....
Gulf and Pacific Coast, Mexico													
Isla Tiburon	....	....	....	....	1	9	10	16	10	4	....	....	....
Isla San Pedro Martir[2]	....	....	....	....	....	9	6	8	10	4	....	1	....
Isla San Pedro Nolasco	....	....	....	....	....	....	1	1	....	1	1	....	....
Bahia San Pedro	....	....	....	....	....	2	7	5	....	1	....	1	....
Guaymas and environs	....	....	1	4	12	38	58	70	39	20	9	6	1
M. h. polyporosus													
Punta Camaron	....	....	1	....	....	2	....	....	....	....	....	....	....
Mazatlan[1]	3	7	30	22	20	5	2	1	....	....	....	....	....
Chamela	....	....	....	....	1	....	....	....	....	....	....	....	....
Cleophas (Tres Marias)	....	....	....	1	....	....	....	....	....	....	....	....	....
Acapulco	....	....	....	1	....	....	....	....	....	....	....	....	....

[1] Including adjacent islands.
[2] Arbitrarily included here.

Scales never present on midline before dorsal; present or absent on prepectoral area and breast of adult of *M. h. hubbsi;* always present on prepectoral area and breast of adults of *M. h. polyporosus.*

There are two to four preopercular canals (the most ventral of which may be present only as a pore) extending onto the opercle, the longest of which extends from two-fifths to three-fifths the distance across the opercle.

Color pattern is variable with sex and locality. Specimens of *M. h. hubbsi* vary geographically and within a series more than do those of *M. h. polyporosus.* The most striking character demonstrating this is represented in Plate VI, Figure 4 showing extremes in color pattern of the ventral side of the head. Some specimens of *M. h. hubbsi* show the spotted condition which is present in *M. h. polyporosus,* but in no specimen of *M. h. polyporosus* is the underside of the head barred. The barred pattern, or some recognizable variation of it, always constitutes a large, if not the largest, percentage of ventral head patterns present in any series of *M. h. hubbsi.*

There is a spot almost always present at the base of each pelvic fin.

TABLE 6

Frequency Distributions of Symphysial Pores in Specimens of *Malacoctenus hubbsi* Over 40 mm. in Standard Length

	1	2	3	4	5	6	7	8	9	10
M. h. hubbsi										
Pacific Coast, Baja California										
Puerta Mala Arrima	46	10	6	....	....	....	....	....	....	....
Bahia Magdalena	51	25	28	6	....	....	....	....	....	....
Gulf Coast, Baja California[1]										
Isla Mejia	13	7	13	4	....	....	....	....	....	....
Isla Angel de la Guarda	13	13	20	3	....	....	....	....	....	....
Isla Partida	12	7	25	10	1	....	....	....	....	....
Bahia San Francisquito	59	36	40	4	....	....	....	....	....	....
Bahia San Carlos	9	4	7	2	1	....	....	....	....	....
Isla Santa Inez	2	....	1	....	....	....	....	....	....	....
Bahia Santa Inez	13	15	24	8	....	1	....	....	....	....
Isla Ildefonso	24	18	20	3	....	....	....	....	....	....
Isla Coronado	..	....	1	....	....	....	....	....	....	....
Isla Monserrate	1	3	3	1	....	....	....	....	....	....
Bahia Agua Verde	....	4	3	4	....	....	....	....	....	....
Isla Espiritu Santo	....	....	1	....	....	....	....	....	....	....
Isla Cerralvo	....	2	1	....	....	....	....	....	....	....
Bahia de los Muertos	2	4	2	....	....	....	..	....	....	....
Punta Frailes	2	2	2	1	....	....	....	....	....	....
San Lucas	....	1	2	..	....	....	....	....	....	....
Gulf and Pacific Coast, Mexico										
Isla Tiburon	19	18	18	4	....	....	....	....	....	....
Isla San Pedro Martir[2]	11	7	12	1	....	....	....	....	....	....
Isla San Pedro Nolasco	2	..	3	....	....	....	....	....	....	....
Bahia San Pedro	8	1	7	1	....	....	....	....	....	....
Guaymas and environs	126	72	113	23	....	....	....	....	....	....
M. h. polyporosus										
Punta Camaron	....	..	..	....	1	2	....	....	....	....
Mazatlan[1]	....	1	10	14	26	21	20	5	3	1
Cleophas (Tres Marias)	....	....	....	....	....	....	....	....	1	....

[1] Including adjacent islands.
[2] Arbitrarily included here.

Males of both subspecies are usually separable from females by having a more uniform coloration and decreased, or usually absent. spotting of the dorsal, anal. and caudal fins.

Other particulars of coloration can be determined from the photographs.

Relationship. Malacoctenus hubbsi appears to be most closely related to a group of species comprising also *M. zacae, M. costaricanus, M. zonifer, M. zonogaster,* and *M. ebisui,* in the Pacific and *M. triangulatus* in the Atlantic. It can be distinguished from the Pacific forms by the characters given in the key. It differs from *M. triangulatus* in lacking scales on the midline before the dorsal, in having the length of the shortest pelvic ray contained in the longest fewer times, and in coloration.

Holotype. See nominal typical subspecies.

MALACOCTENUS HUBBSI HUBBSI, New Subspecies

(Plate VI, Figs. 1, 2, and 4)

Malacoctenus delalandi, Osburn and Nichols, 1916: 178* (not of Valenciennes).
Malacoctenus, new species Barnhart and Hubbs, 1946: 371*.

This subspecies is separated from *M. h. polyporosus* under the account for that subspecies.

In Table 6 it can be seen that there is a bimodality of the symphysial pores at the 1 and 3 frequencies for this subspecies. Young specimens always have one centrally located pore. If more pores are formed at a later stage they usually appear as a pair rupturing simultaneously. The number of pores present appears to be stabilized by the time the individual attains 40 mm.

Barnhart and Hubbs (1946) referred to Osburn and Nichols' (1916) specimen of *Malacoctenus*, from Cedros Island in Bahia San Sebastian Vizcaino, as a new species. Although this specimen has not been seen, the only specimens of *Malacoctenus* known from localities that far north on the Pacific coast are those of *M. h. hubbsi*.

Holotype. SU 49651, an adult male, 57.3 mm. in standard length, from the southwest end of Isla San Pedro Martir, Gulf of California, Mexico. Collected by J. Böhlke and party, May 4, 1952 (Field number: 34–TP–2).

Paratypes. Two thousand five hundred ninety-three specimens. Nine hundred sixty-four from Puerto Mala Arrima, Bahia Sebastian Vizcaino, Baja California, Pacific coast: UCLA W51–221, W51–223–4; 246 from Bahia Magdalena, Baja California, Pacific coast: SU 49659–60, UCLA W55–85, W55–93–4; 39 from Isla Mejia, Gulf of California: SU 49668; 95 from Isla Angel de la Guarda, Gulf of California: UCLA W54–258, W54–262, W56–20; 145 from Isla Partida, Gulf of California: SU 18932, 49669, UCLA W56–22; 136 from Bahia San Francisquito, Baja California, Gulf coast: SU 49670–72; 24 from Moreno Rocks, Bahia San Carlos, Baja California, Gulf coast: 49664; 3 from Isla Santa Inez, Baja California, Gulf coast: SU 49657–58; 137 from Bahia Santa Inez, Baja California, Gulf coast: BMNH 1957.5.1.150–204, SU 18935, 49655–56, UCLA W53–91; 1 from Bahia Coyote, Bahia Conception, Baja California, Gulf coast: UCLA W53–97; 67 from Isla Ildefonso, Gulf of California: SU 19182, 49673–75; 1 from Isla Coronado, Gulf of California: SU 18769; 8 from Isla Monserrate, Gulf of California: SU 49665; 11 from Bahia Agua Verde, Baja California, Gulf coast: SU 18934; 2 from Isla Espiritu Santo, Gulf of California: CAS 20719, SU 49654; 5 from Isla Cerralvo, Gulf of California: SU 49663; 8 from Bahia de los Muertos, Baja California, Gulf coast: SU 49662; 7 from Punta Frailes, Baja California, Gulf coast: UCLA W52–263; 6 from Cape San Lucas, Baja California: SU 49676, USNM 134904, UCLA W55–118; 111 from Isla Tiburon, Gulf of California: USNM 174965, SU 49653, 49667; 43 from Isla San Pedro Martir, Gulf of California: SU 49652 (parachronotopotypes); 6 from Isla San Pedro Nolasco, Gulf of California: SU 18968, 49666; 17 from Bahia San Pedro, Sonora: SU 18969; 521 from Guaymas

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PLATE VI

Arranged Top to Bottom

FIG. 1. *Malacoctenus hubbsi hubbsi*, SU 49652, an adult male, 58.5 mm. in standard length, from Bahia San Carlos, Baja California, Mexico.

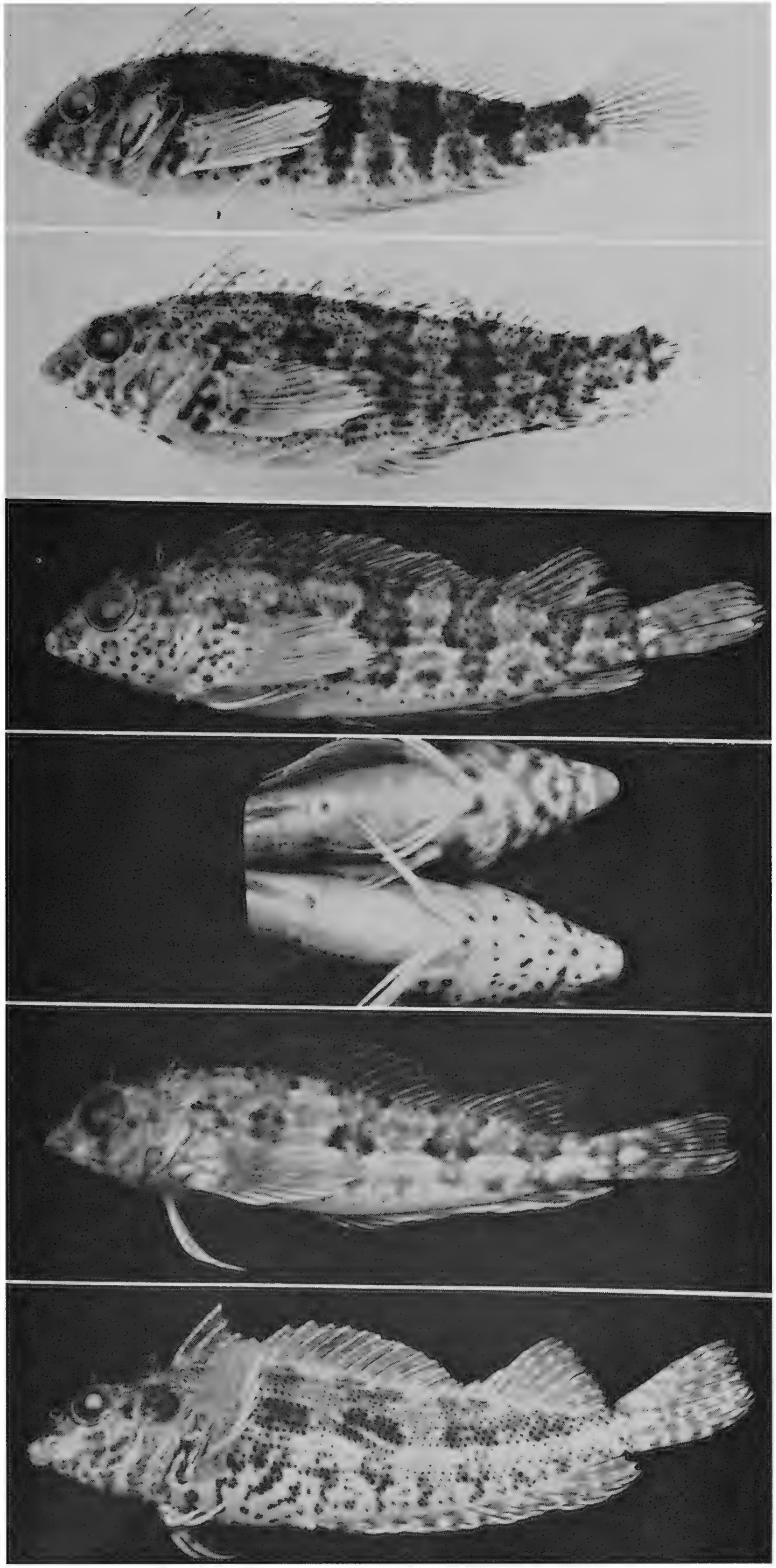
FIG. 2. *Malacoctenus hubbsi hubbsi*, SU 49664, an adult female, 57 mm. in standard length, from Bahia San Carlos,Baja California, Mexico.

FIG. 3. *Malacoctenus hubbsi polyporosus*, UCLA W51–20, an immature male, 49 mm. in standard length, from the Islas Venados, north of Mazatltan, Sinaloa, Mexico.

FIG. 4. Ventral view of *Malacoctenus h. hubbsi* (upper) and *Malacoctenus h. polyporosus* (lower) showing coloration of ventral side of head.

FIG. 5. *Malacoctenus zacae*, SU 49685, holotype, an adult male, 43.8 mm. in standard length, from Puerto Marques, Guerrero, Mexico.

FIG. 6. *Malacoctenus zonogaster*, SU 37583, an adult female, 58.5 mm. in standard length, from James Island, Galapagos.



and environs, Sonora: CAS 20720, SU 16654, 16564, 16514, 16522, 16573, 49661, CNHM 42685, 50254, 61902.

I take pleasure in naming this species for Dr. Clark Hubbs in recognition of his contributions to the study of clinid systematics.

MALACOCTENUS HUBBSI POLYPOROSUS, New Subspecies

(Plate VI, Figs. 3 and 4)

This subspecies differs from *M. h. hubbsi* most prominently in having a higher average number of symphysial pores (Table 6), in having a lower average number of lateral line scales (Table 5), and a lower average number of anal rays (see *Description* under species).

The two subspecies are entirely allopatric: *M. h. hubbsi* is known only from the Gulf of California coast of Mexico as far south as Guaymas, the Gulf and Pacific coasts of Baja California, and the islands of the Gulf of California; *M. h. polyporosus* is known only from the coast of the Mexican mainland from Punta Camaron, north of Mazatlan, to Acapulco and the Islas Tres Marias.

Holotype. USNM 174957, an adult male, 51 mm. in standard length, from the Islas Venados, just north of Mazatlan, Sinaloa, Mexico. Collected by G. Bartholomew and K. Norris, February 26, 1951 (Field number: W51–26).

Paratypes. Four hundred ninety-nine specimens. Three from Punta Camaron, Sinaloa: UCLA W51–44; 8 from Mazatlan, Sinaloa: UCLA W51–58; 485 from the Islas Venados: ANSP 74511, BMNH 1957.5.1.90–149, CNHM 61898, UCLA W51–20, W51–29, W51–54, USNM 174960 (parachronotopotypes); 1 from Chamela, Jalisco: SU 49677; 1 from Acapulco, Guerrero: SU 49679; 1 from Isla Maria Cleophas, Tres Marias: SU 49678.

Named *polyporosus* for its many symphysial pores.

MALACOCTENUS COSTARICANUS, New Species

(Plate VII, Fig. 1)

Description. Fin rays: dorsal XIX, 11; anal II, 19; pectorals 13 or 14 (14). Lateral line 50 or 51. Gill-rakers 10 or 11. Symphysial pores 4 and 7.

Head 27.6 to 30.0 percent of standard length in specimens over 28 mm. Bony orbital diameter 8.4, 8.0, 10.4, 10.6, and snout length 8.8, 8.4, 9.7, 8.8 percent of standard length respectively in specimens 51.2, 49.8, 28.8, 28.3 mm. First dorsal spine more than 11 percent of standard length; exceeding second through fifth and last four dorsal spines; sometimes exceeding tenth. Length of shortest pelvic ray contained 1⅘ to 2 times in longest. Interspace between bases of nuchal cirri contained more than four

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PLATE VII

Arranged Top to Bottom

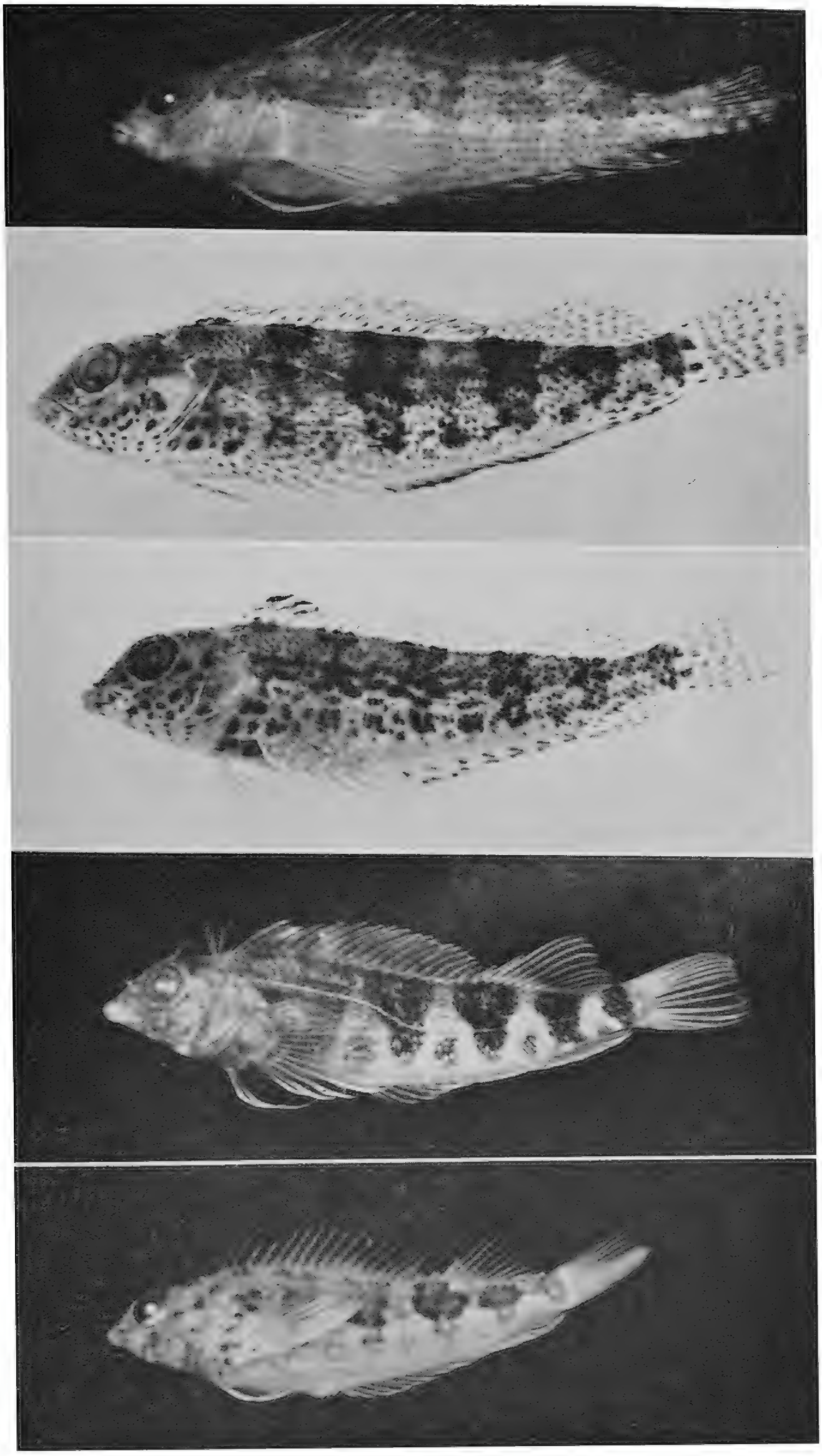
FIG. 1. *Malacoctenus costaricanus*, SU 49601, holotype, an adult female, 49.8 mm. in standard length, from Piedra Blanca Bay, Costa Rica.

FIG. 2. *Malacoctenus zonifer zonifer*, UCLA W51–52, an adult female, 58.5 mm. in standard length, from the Islas Venados, north of Mazatlan, Sinaloa, Mexico.

FIG. 3. *Malacoctenus zonifer sudensis*, SU 49707, an adult female, 49 mm. in standard length, from the Gulf of Nicoya, Costa Rica.

FIG. 4. *Malacoctenus triangulatus*, ANSP 74729, holotype, an adult male, 45 mm. in standard length, from New Providence Island, Bahamas.

FIG. 5. *Malacoctenus ebisui*, SU 49614, an adult female, 31.3 mm. in standard length, from Bahia Honda, Panama.



times in a single base. Maxillary length 9.2 to 10.6 percent of standard length. Largest specimen 51.2 mm.

Scales present on midline before dorsal, on ventral margin of prepectoral area, and sometimes on breast.

There are three preopercular canals extending onto the opercle, the middle one of which is the longest, and extends three-fifths to two-thirds the distance across the opercle.

There are six irregular bands on the body, much darker above the midline of the body. These bands extend slightly onto the dorsal. The body is noticeably lighter below the midline. There are numerous small spots in longitudinal series on the body, most noticeable below the midline of the body in the adults; absent in the young. The head is light and unmarked except for some dark spots behind the eye and on the dorsal portions of the preopercle and opercle. The membranes of the anterior three dorsal spines are the darkest. The dorsal has some dark spots distally on the sixth from the last spine. Other dark spots are found, distally on the first two dorsal rays. The anal is marked with dusky spots. The caudal is irregularly barred (barring absent in the small specimens) and has dark spots distally on the uppermost and lowermost two rays. The pectorals and pelvics are unmarked.

Relationship. Malacoctenus costaricanus appears to belong to a group of species including *M. hubbsi*, *M. zacae*, *M. ebisui*, *M. zonifer*, and *M. zonogaster*, in the Pacific, and *M. triangulatus* in the Atlantic. It can be distinguished from the Pacific species by characters given in the key. It differs from *M. triangulatus* in dorsal and anal formulae, number of symphysial pores, number of times the length of the shortest pelvic fin is contained in the longest, and in coloration.

Holotype. SU 49601, an adult female, 49.8 mm. in standard length, from Piedra Blanca Bay, Costa Rica. Collected by the New York Zoological Society Zaca Expedition, February 2, 1938 (Original number 28151).

Paratypes. Three specimens. Two parachronotopotypes: SU 49602; 1 paratopotype: SU 49603.

Named *costaricanus* because it is known only from Costa Rica.

MALACOCTENUS ZACAE, New Species

(Plate VI, Fig. 5)

Description. Fin rays: dorsal XX, 9 to 11 or XXI, 9 or 10 (XX, 10 in 75 percent of specimens); anal II, 18 to 20 (19); pectorals 14. Lateral line 50 to 55. Gill-rakers 9 to 11. Symphysial pores 3 to 15 (4 to 8).

Head 26.0 to 31.2 percent of standard length in specimens over 16.5 mm. in standard length. Bony orbital diameter larger than snout in specimens under 40 mm.; equal to or larger than snout in specimens over 40 mm. Either of these measurements attaining 10 percent of standard length only rarely in specimens over 30 mm. First dorsal spine always exceeding 10 percent of standard length (see *Discussion* below); usually exceeding all other dorsal spines, except in specimens from Mazatlan south; here occasionally exceeded by tenth dorsal spine. Length of shortest pelvic ray contained 1½ to 1¾ times in longest. Interspace between nuchal cirri bases contained more than 3 times (sometimes bases meet in midline) in a single base. Maxillary length 8.7 to 9.6 percent of standard length. Largest specimen 47 mm.

Scales not present on midline before dorsal or on prepectoral area; a few sometimes encroaching on breast.

There are three (rarely four) preopercular canals extending onto the opercle, the two more ventral of which are of about equal length and extend one-half to three-quarters the distance across the opercle. Frequently the upper half of the opercle is covered by a branching network of these canals.

I could detect no differences between the coloration of males and females, although individual specimens may show considerable variation.

The dorsal may or may not be spotted. The membranes of the anterior three spines are the darkest. There is usually a concentration of pigment distally on the anterior two or three soft rays. There are spots or dusky areas on the dorsal above the bands on the body. The anal may be unmarked or barred with dusky. The caudal is clear or with irregular elongate spots on the rays. There are frequently concentrations of pigment at the tips of the upper and lower rays. The pectorals are clear with some dusky areas at the bases of the more ventral rays. The pelvics are unmarked. The body has five or six irregular, triangular-like bands with their bases dorsal. The bands are usually darkest in their midportions and lightest below the midline of the body. They are frequently indicated as dusky areas outlined by pairs of darker blotches dorsally, medially, and ventrally. The interspaces between the bands are dusky above and lighter below the midline, with irregular markings below the midline. The venter is unmarked, and only very rarely are there dark spots at the bases of the pelvic fins. The ventral portion of the head is unmarked or delicately specked. The sides of the head may be uniformly dusky, marked with distinct lines and blotches, or with three or four "spokes" radiating from each orbit. Frequently there is a dark quasi-circle on the lower half of the opercle with lines extending ventrally from it. A similar mark may appear on the prepectoral area. There is usually a branched stripe extending beneath the orbit.

Discussion. There appears to be a north-south cline in the length of the first dorsal spine when recorded as percent of standard length (Table 7). However, when more specimens are known it may be that two subspecies are present: one from Baja California and the Gulf coast of Mexico, and the other on the Pacific coast of Mexico from Mazatlan southward. In northern specimens the spine reaches its maximum length.

TABLE 7

Frequency Distributions of First Dorsal Spine Lengths Recorded as Percent of Standard Length in *Malacoctenus zacae*

Upper Class Limits	10.9	11.9	12.9	13.9	14.9	15.9	16.9	17.9
Arroyo Seco, Pacific Coast, Baja California	....	....	....	....	....	....	3	1
Los Frailes, tip of Baja California	....	....	1	....	1	1	....	....
San Lucas, tip of Baja California	2	....	....	4	4	2	1	....
Mazanillo, Colima	....	1	1	....	....	....	....	....
Acapulco, Guerrero	4	13	8	6	....	....	....	....
Puerto Marques, Guerrero	1	5	2	1	....	....	....	....

Relationship. This species is most closely related to a group comprising also in the Pacific *M. hubbsi, M. ebisui, M. zonifer, M. costaricanus,* and *M. zonogaster,* and in the Atlantic, *M. triangulatus.* It can be distinguished from the Pacific forms by characters given in the key. It differs from *M. triangulatus* in having typically lower counts for the dorsal and anal fins, in not having the prepectoral area scaled, in not having scales on the midline before the dorsal, and in the number and nature of the preopercular canals extending on the opercle.

Holotype. SU 49685, an adult male, 43.8 mm. in standard length, from Puerto Mar-

ques, south of Acapulco, Guerrero, Mexico. Collected by C. L. Hubbs, Zaca Expedition, September 10, 1946 (Field number: H 46–239).

Paratypes. Sixty-eight specimens from Mexico. Eight parachronotopotypes: SU 49686; 1 paratopotype: SU 49688; 35 from Acapulco, Guerrero: SU 49687, USNM 174966; 2 from Mazanillo, Colima: UMMZ 171895; 14 from the vicinity of Cape San Lucas, Baja California: CNHM 61899, SU 49690; 4 from Frailes Bay, Baja California (east coast): BMNH 1957.5.1.88–89, UCLA W52–263; 4 from three miles north of Arroyo Seco, Baja California (west coast): SU 49689.

Named *zacae* for the Zaca Expedition.

MALACOCTENUS ZONOGASTER Heller and Snodgrass

(Plate VI, Fig. 6)

Labrosomus delalandi, Gilbert, 1890: 452 (not of Valenciennes).

Malacoctenus zonogaster Heller and Snodgrass, 1903: 217; Snodgrass and Heller, 1905: 420; Kendall and Radcliffe, 1912: 152; Herre, 1936: 403; Fowler, 1938: 259; Seale, 1940: 39; Fowler, 1944: 521; Hubbs, 1952: 105.

Malacoctenus delalandi, Borodin, 1928: 32* (not of Valenciennes).

Description. Fin rays: dorsal XX, 12; XXI 10 to 12; or XXII, 10 or 11 (XXI, 11 in 82 percent of specimens); anal II, 20 to 22 (21); pectorals 14. Lateral line 57 to 64 (59 to 62). Gill-rakers 10 to 13. Symphysial pores 1 to 14 (3 to 8).

Head length 26.2 to 29.0 percent of standard length in specimens over 26 mm. Bony orbital diameter sometimes exceeding 10 percent of standard length; larger than snout in specimens over 40 mm.; usually smaller than snout in specimens over 50 mm. Snout length never attaining 10 percent of standard length. First dorsal spine usually exceeding 12.5 percent of standard length; always exceeding all other dorsal spines. Length of shortest pelvic ray contained 1½ to 2⅓ times in longest. Interspace between nuchal cirri bases contained 2 to 5 times in a single base. Maxillary length 7.9 to 9.3 percent of standard length. Largest specimen 69.2 mm.

Scales sometimes present on midline before dorsal and on breast; never present on prepectoral area.

There are from two to five, usually two or three, preopercular canals extending onto the opercle, the more ventral of which is the longest and extends from one-third to one-half the distance across the opercle.

Color pattern is variable with sex. Males have the dorsal clear or dusky with few or no dark spots. The membranes of the anterior three dorsal spines are darker than the others. The anal is dusky, becoming darker at its distal margin. The caudal is spotted; the pectorals are dusky with a few dark spots on the proximal portions of the ventral rays. The pelvics are variably marked, but the innermost ray is always dark. There are six irregular bands on the body which are uniformly dark. The interspaces between the bands are dusky with little or no indications of spotting. The venter is light or dusky without conspicuous markings on the midportions. The ventral portion of the head is darkly mottled or barred. The sides of the head are mottled. There is a conspicuous dark blotch on the upper third of the opercle, below which is a slightly smaller light area.

Females have the dorsal, anal, and caudal densely spotted. The membranes of the first three dorsal spines are like those of the male. The pectorals are dusky and spotted, especially on the proximal portions of the ventral rays. The pelvics are like those of the

male. There are six irregular bands on the body which are sometimes interrupted and always lighter below the midline of the body. The interspaces between the bands are conspicuous for rows of small dark spots, lighter below the midline of the body, and containing irregular marks. In larger females the venter is darkly spotted or lined over its entire area. In smaller females the spotting does not extend across the venter. The sides of the head are as in the male. Specimens of 16 mm. show indications of adult coloration.

Relationship. Malacoctenus zonogaster appears to belong to a group comprising in the Pacific *M. hubbsi, M. zacae, M. costaricanus, M. zonifer, M. ebisui,* and in the Atlantic, *M. triangulatus.* It can be distinguished from the Pacific forms by characters given in the key. It differs from *M. triangulatus,* in lacking scales on the prepectoral area, in having the length of the shortest pelvic ray contained fewer times in the longest, and in coloration.

Material. Two hundred nineteen specimens were examined from localities throughout the Galapagos Islands, to which area this species is restricted: AMNH 3530, BMNH 1938.12.12.111–112, CAS 3062–63, 3124–25, 3681–84, 4088–89, 4497–4505, 4965–68, 5347, 5497, 6905, CNHM 24876–24918, MCZ 29410, SU 24378, 24390, 24397–98, 37581–85, 37588, UCLA W53–16, W53–152, W55–314, USNM 38297, 65568, 107111.

MALACOCTENUS ZONIFER (Jordan and Gilbert)

(For synonymy see subspecies)

Description. Fin rays: dorsal XIX, 11 or 12; XX, 10 to 12; or XXI, 11 (XX, 11 in 85 percent of specimens); anal II, 17 to 21 (19 or 20); pectorals 13 or 14 (14). Lateral line 52 to 60 (54 to 58). Gill-rakers 9 to 13 (10 to 12). Symphysial pores 1 to 20.

Head 26.4 to 30.0 percent of standard length in specimens over 22 mm. Bony orbital diameter usually smaller than snout in specimens over 40 mm.; usually larger than snout in specimens less than 35 mm. Either of these measurements rarely attaining 10 percent of standard length in specimens over 40 mm. Length of first dorsal spine usually less than 10 percent of standard length (always less than 11 percent); always exceeding third, fourth, and last four dorsal spines; always exceeded by tenth dorsal spine; sometimes exceeded by second and fifth dorsal spines. Length of shortest pelvic ray contained 1⅕ to 1¾ times in longest. Interspace between nuchal cirri bases contained 1½ to 4 times in a single base. Maxillary length 9.2 to 10.5 percent of standard length. Largest specimen 68 mm.

Scales present on midline before dorsal; absent on prepectoral area; sometimes present on breast, more frequently in males than females.

There are two or three preopercular canals extending onto the opercle, the more ventral of which is usually the longest and extends one-sixth to two-fifths the distance across the opercle.

Coloration is described under each subspecies.

Relationship. This species is most closely related to a group in the Pacific comprising *M. hubbsi, M. costaricanus, M. zacae, M. zonogaster,* and *M. ebisui,* and in the Atlantic, *M. triangulatus.* It can be distinguished from the Pacific forms by the characters given in the key. It differs from *M. triangulatus* in having the length of the shortest pelvic ray contained fewer times in the longest, in typical dorsal and anal formulae, in number of symphysial pores, and in coloration.

MALACOCTENUS ZONIFER ZONIFER (Jordan and Gilbert)
(Plate VII, Fig. 2)

Clinus phillipi, Lockington. 1881: 114* (not of Steindachner).
Clinus zonifer Jordan and Gilbert, 1882b: 361; Jordan and Gilbert, 1883: 108.
Labrosomus zonifer, Jordan, 1885: 389; Jordan, 1887b: 908.
Labrisomus delalandi, Jordan, 1889: 333* (not of Valenciennes).
Labrosomus delalandi, Jordan, 1895: 501 (not of Valenciennes).
Malacoctenus delalandi, Jordan and Evermann, 1898: 2358 (not of Valenciennes); Ribeiro, 1915: 7 (not of Valenciennes); Jordan, Evermann, and Clark, 1930: 459 (in part; not of Valenciennes).
Malacoctenus delalandii, Kendall and Radcliffe, 1912: 151 (in part; not of Valenciennes).
Malacoctenus zonifer, Hubbs, 1952: 104 (in part).

This subspecies is separated from *Malacoctenus z. sudensis* under the account for that subspecies.

There are slight differences in coloration between males and females. Adult males have the head more uniformly dark than do females. Usually the dark opercle is divided by a light, narrow arched line. Females have the head spotted ventrally; the spots extend onto the branchiostegal membranes, but do not extend across the gular fold. The opercle in females usually exhibits two spots ventrally which are larger than any of the others on the head. The dorsal, caudal, and pectorals are spotted in both sexes, though less so in males. The membranes of the anterior four dorsal spines have a concentration of pigment ventrally, which is less intense or absent dorsally. The anal of males is dusky, that of females spotted. The pelvics of both sexes are clear, except for the innermost ray which is dusky or spotted. There are five dark bands on the body, the first four of which do not extend ventrally as far as the anal base. The interspaces between the bands are much darker above the midline of the body, due primarily to an increased density of the scale markings. The venter is uniformly light. The prepectoral area is spotted.

The type material of this subspecies consists of three specimens, all females. In two of these (USNM 164585) the anal elements total 22; in the third specimen (USNM 28122) the anal elements total 21. This latter specimen is here designated lectotype.

This subspecies is known only from the coasts of Mexico and the adjacent islands; only one specimen is known from north of Mazatlan.

Material. Three hundred sixty-nine specimens were examined. One from La Paz, Baja California: SU 2982; 159 from Mazatlan and adjacent islands (Islas Venados), Sinaloa: BMNH 95.5.27.152, 95.5.27.154, CAS 6040, SU 2981, 49717, UCLA W51–20, W51–26, W51–29, W51–33, W51–52, USNM 28122, 37159, 47421, 164585; 9 from Cleophas Island, Tres Marias: SU 49718; 6 from Chamela and adjacent islands, Jalisco: SU 49709–11; 61 from Mazanillo, Colima: AMNH 15858, UMMZ 171892; 100 from Acapulco, Guerrero: MCZ 29607, SU 49719, UCLA W56–17; 2 from Puerto Marques, Guerrero: SU 49720; 9 from Puerto Angeles, Oaxaca: SU 49712; 19 from Puerto Guatulco, Oaxaca: SU 49713–15; 4 from Tangola-Tangola, Oaxaca: SU 49708, 49716.

MALACOCTENUS ZONIFER SUDENSIS, New Subspecies
(Plate VII, Fig. 3)

Clinus delalandii, Günther, 1861a: 371 (in part); not of Valenciennes); Günther, 1861b: 264 (in part; not of Valenciennes); Boulenger, 1899: 8* (not of Valenciennes).

Malacoctenus delalandi Gilbert and Starks, 1904: 189* (not of Valencinennes); Borodin, 1928: 32* (not of Valenciennes); Seale, 1940: 38 (in part; not of Valenciennes).

Malacoctenus delalandii, Kendall and Radcliffe, 1912: 151 (in part; not of Valenciennes).

Malacoctenus zonifer, Meek and Hildebrand, 1928: 940; Nichols and Murphy, 1944: 255*; Fowler, 1944: 521*; Tortonese, 1951: 113; Hubbs, 1952: 104 (in part).

Malacoctenus z. sudensis differs from *M. z. zonifer* in having the dorsal portions of the membranes of the first three or four dorsal spines always heavily pigmented, in having a higher average number of symphysial pores at any particular length (Table 8), in having a higher average number of gill-rakers and total anal elements (Table 9), in having a lesser degree of sexual dimorphism of coloration (males have a spotted anal fin and frequently two spots ventrally on the opercle), and in the presence of spots on the gular fold of many adults.

The basic color pattern is the same as that of *M. z. zonifer*, but differs as mentioned above and in having the spots on the head, body, and fins somwhat larger; occasionally

TABLE 8

Frequency Distributions of Symphysial Pores in *Malacoctenus z. zonifer* (Italicized) and *M. z. sudensis* Grouped by Standard Length Intervals of 5 Millimeters

Pores	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
S.L.																				
	24	*2*																		
15–19.9																				
			1	1	1															
	3	*1*	*1*	*1*																
20–24.9																				
			3	4	5															
		2	*7*	*2*																
25–29.9																				
			4	4	5	3														
		3	*10*	*3*	*3*															
30–34.9																				
					11	4	3													
			9	*13*	*2*															
35–39.9																				
					1	7	11	4	1											
		1	*9*	*11*	*3*	*1*	*1*													
40–44.9																				
					3	4	7	5	1	2	1									
			2	*16*	*11*			*1*												
45–49.9																				
						3	9	12	6	10	2	3	1			1				
			8	*23*	*20*	*9*	*2*	*2*												
50–54.9																				
						2	5	3	7	5	8	1	2	3	2	4	1	1		
			2	*15*	*22*	*11*	*7*		*1*											
55–59.9																				
							1	3	1	2		2		1						2
			4	*5*	*6*															
60–64.9																				
												1								
			1	*1*	*1*		*1*													
65–69.9																				

TABLE 9

Frequency Distribution of Gill-rakers and Total Anal Elements in *Malacoctenus zonifer*

	Gill-rakers					Anal Elements				
	9	10	11	12	13	19	20	21	22	23
zonifer										
La Paz, Baja California	....	....	....	1	....	....	....	....	1	....
Mazatlan, Sinaloa	2	18	55	7	....	....	....	28	61	....
Chamela, Jalisco	....	....	4	....	....	....	....	....	6	....
Mazanillo, Colima	....	7	30	9	....	....	....	19	41	....
Acapulco, Guerrero	....	5	40	5	....	1	1	23	71	....
Port Guatulco, Oaxaca	....	....	6	1	....	....	1	12	6	....
Tangola-Tangola, Oaxaca	....	....	3	....	....	....	....	....	4	....
Las Tres Marias	....	....	4	5	....	....	....	1	8	....
sudensis										
Nicaragua	....	2	10	4	.	....	1	2	21	1
Costa Rica	....	14	26	26	2	....	1	11	61	3
Panama	.	6	53	55	4	....	....	17	132	....
Colombia	....	....	3	....	1	....	....	....	5	....
Ecuador	....	....	8	....	2	....	....	....	10	....

there may be a few spots on the venter. The bands on the body are less uniformly colored.

In specimens as small as 15.5 mm. the dark pigmentation of the anterior membranes of the dorsal fin is recognizable, and this alone is sufficient to identify young of this subspecies from all other labrisomines.

This subspecies is known only from the Pacific coasts and adjacent islands of Central and South America south of the Gulf of Fonseca and north of Peru. It is separated from *M. z. zonifer* of the north by approximately seven hundred miles of coastline from which no clinids are known.

Holotype. *SU* 49691, an adult male, 49.8 mm. in standard length, from Saboga, Perlas Islands, Panama. Collected by the Antares Expedition of the New York Zoological Society, June 27, 1933 (Original number: 24200).

Paratypes. Three hundred forty-four specimens. Sixteen from Corinto, Nicaragua: SU 49695–96; 4 from Brito, Nicaragua: ANSP 10574–10577; 5 from San Juan del Sur, Nicaragua: SU 49697; 8 from Port Parker, Costa Rica: SU 49698, 49700; 19 from Piedra Blanca, Costa Rica: SU 49702–04; 4 from Port Culebra, Costa Rica: SU 49701; 17 from the Negritos Islands, Gulf of Nicoya, Costa Rica: SU 49707; 28 from Braxilito Bay, Costa Rica: CAS 4014–41; 1 from Balboa, Canal Zone: USNM 81898; 1 from Bahia Honda, Panama: SU 49706; 1 from La Venta, Panama: USNM 144828; 10 from Piñas Bay, Panama: USNM 101933; 1 from Bella Vista Reef, Panama: USNM 144825; 27 from Saboga, Perlas Islands: SU 49692 (parachronotopotypes), USNM 144824, 174963; 10 from Pacheca, Perlas Islands: CAS 6987, SU 49693; 170 from San Jose, Perlas Islands: BMNH 1957.5.1.1–50, CNHM 61898, UCLA W53–283, USNM 144820, 144822, 128493; 1 from Isla Parida, Panama: SU 49705; 2 from the Secas Islands, Panama: USNM 102002; 1 from Perico Island, Panama: USNM 65567; 2 from Tabogella Island, Panama: USNM 144826; 3 from Port Utria, Colombia: USNM 101936, 101990; 1 from Cobita Bay, Colombia: CAS 6907; 1 from Corrientes bay, Colombia: USNM 94046; 2 from Manta, Ecuador: USNM 101987–88; 3 from St. Helena Bay, Ecuador: BMNH 98.12.31.44–46.

Named *sudensis* because it occupies the southern part of the range of the species.

MALACOCTENUS TRIANGULATUS, New Species

(Plate VII, Fig. 4)

Malacoctenus versicolor, Longley and Hildebrand, 1941: 248 (not of Poey).
Malacoctenus puertoricensis, Fowler, 1950: 84 (not of Evermann and Marsh).
Malacoctenus delalandei, Smith, 1957: 14 (not of Valenciennes).

Description. Fin rays: dorsal XIX, 12 or 13; XX, 11 to 13; or XXI, 11 (XX, 12 in 81 percent of specimens); anal II, 20 to 22 (21); pectorals 13 to 15 (14). Lateral line 52 to 61. Gill-rakers 11 to 14. Symphysial pores 1 to 3 (1 or 2).

Head 26 to 30 percent of standard length in specimens over 26 mm. Bony orbital diameter 8.3 to 11.5 percent of standard length in specimens over 26 mm.; rarely shorter than snout length. First dorsal spine rarely less than 10 percent of standard length (usually more than 11 percent), always exceeding next three and last four dorsal spines, which are usually less than 10 percent of standard length. Length of shortest pelvic ray contained 2⅛ to 3⅛ times in longest. Interspace between nuchal cirri bases contained 1⅕ to 3½ times in a single base. Maxillary length 8.2 to 10.6 percent of standard length. Largest specimen 48 mm.

Scales present on midline before dorsal and on prepectoral area; absent on these areas in young, but very rarely in adults. Breast usually scaled in adult males; usually naked in adult females. The last scale in the lateral line series frequently without a pore.

There are two preopercular canals extending onto the opercle, the more ventral of which extends from one-quarter to one-half the distance across the opercle.

There is considerable variation in the color pattern between individuals. The most common pattern consists of five or six subtriangular, saddle-like markings on the body, with their bases on the dorsal contour. The saddles may be dark, almost as light as the color of the interspaces between them, or in rare specimens entirely absent (body without color). The saddles may be uniformly colored, embody a reticulate pattern of light lines, or be indicated in outline only by dark spots. The ventral apices of the saddles may appear abruptly constricted below the midline of the body. The most anterior saddle may be more heavily pigmented than the rest and extend onto the anterior dorsal spines as a conspicuous black blotch. The interspaces may be uniformly light or have dusky triangular patches present.

The fins of mature males are clear or lightly dusky, with occasional specimens having light spots on the dorsal. The dorsal, anal, and caudal fins of females are lightly to heavily spotted.

The venter is usually light to dusky. Many specimens have a dark line extending from the prepectoral area of one side across the prepelvic area to the prepectoral area of the other side. The prepelvic area may be uniformly dark in males. The ventral side of the head is light or with alternating dark and light bars, most distinctly represented in males. The sides of the head are light to dusky, with most specimens having two small dark spots on the posterior margin of the circumorbital series. A specimen 16 mm. in standard length from Puerto Rico exhibits adult coloration.

Relationship. Malacoctenus triangulatus appears to be most closely related to a group comprising also the Pacific forms: *M. hubbsi, M. zacae, M. costaricanus, M. zonogaster, M. zonifer*, and *M. ebisui*. It differs from *M. hubbsi* in having scales on the midline before the dorsal, in having the length of the shortest pelvic ray contained a greater number of times in the longest, and in coloration; from *M. zacae* and *M. costaricanus* in the

same characters and in typical dorsal and anal formulae and in the nature of the preopercular pores; from *M. zonogaster* in having scales on the prepectoral area, in the number of times the length of the shortest pelvic ray is contained in the longest, and in coloration; from *M. zonifer* in having the prepectoral area scaled, in the number of times the length of the shortest pelvic ray is contained in the longest, and in coloration; from *M. ebisui* in the same characters as for *M. zonifer* and in having modally higher dorsal and anal formulae. It differs from the other Atlantic forms by those characters given in the key.

Holotype. ANSP 74729, an adult male, 45 mm. in standard length from just west of Delaport Point, New Providence Island, Bahamas (ANSP Station 212), 25° 05′ 04″ north latitude and 77° 27′ 42″ west longitude (H. O. Chart 1377/Nov., 1936). Collected by C. C. G. Chaplin and J. Böhlke, April 11, 1955.

Paratypes. Two hundred sixty-three specimens. Twenty-three from Tortugas, Florida: CNHM 6981, USNM 116823–24, 88120; 177 from the Bahamas: ANSP 72590–91, 74479–93, 74478 (parachronotopotypes), 74531æ43, 74699, 74701æ07 (including one stained); 3 from Cuba: USNM 37430, 82536–37; 5 from Puerto Rico: UMMZ 171181, 171193, 171225, USNM 128794; 5 from Barbados: ANSP 74530; 22 from Isla Fernando Noronha: BMNH 1888.1.19.92–100; 1 from Old Providence Island: ANSP 72684; 1 from the Cayman Islands: BMNH 1939.5.12.179–190; 7 from Campeche Banks, Mexico: CNHM 59878; 3 from Cabo Roja, Vera Cruz, Mexico: IMSC (no number).

Named *triangulatus* for the triangular-like saddles on the body.

MALACOCTENUS EBISUI, New Species

(Plate VII, Fig. 5)

Description. Fin rays: dorsal XIX, 11 or 12; XX, 10 to 12; or XXI, 10 (XX, 11 in 76 percent of specimens); anal II, 18 to 21 (20); pectorals 14: Lateral line 52 to 58. Gill-rakers 11 to 13. Symphysial pores 1 or 2.

Head 24.7 to 30.0 percent of standard length in specimens over 28 mm. Bony orbital diameter always larger than snout; usually exceeding 10 percent of standard length in specimens under 35 mm.; usually less than 10 percent in specimens over 35 mm. Snout always less than 9.5 percent of standard length. First dorsal spine only rarely attaining 10 percent of standard length; never reaching 10.5 percent; always exceeding second, third, fourth, and last four dorsal spines; always exceeded by remaining dorsal spines. Length of shortest pelvic ray contained 1⅗ to 2⅛ times (usually more than 1¾ times) in longest. Interspace between nuchal cirri bases contained 1⅞ to 2⅛ times in a single base. Maxillary length 8.5 to 10.4 percent of standard length. Largest specimen 47 mm.

Scales present on midline before dorsal; not present on prepectoral area; present on breast of males only, becoming fleshy with maturity.

There are two (rarely three) preopercular canals extending onto the opercle, the more ventral of which is the longest and extends from one-half to two-thirds the distance across the opercle.

Color pattern varies with sex and individually. In males all the fins are unmarked, except the caudal, which is frequently spotted. There are five inverted, subtriangular bands on the body, the anterior two of which are reduced in intensity and sometimes absent; the posterior three are frequently fused dorsally. The interspaces between the

bands are either uniformly dusky, or with a few faint markings, and lighter below the midline of the body. The venter is unmarked as is usually the ventral portion of the head, which occasionally has some faint spots. The sides of the head are dusky with a few dark spots.

In females all of the fins are unmarked, except the spinous dorsal and the pectorals of some specimens. The spinous dorsal may be lightly spotted and there may be some dark spots at the bases of the pectoral rays. The bands on the body are variable, but the second and third from the posterior are the most developed. The last band may be absent and the first two bands may be lighter than the rest. The bands are darker dorsally or medianly, and may be uniformly colored or appear as dusky areas outlined by pairs of dark spots. The interspaces between the bands are uniformly dusky dorsally, much lighter below, and contain irregular dark markings. The prepectoral area is variably spotted. The venter is unmarked, but a spot may be present at the base of each pelvic fin. The ventral portion of the head is spotted as are the sides of the head. There are several spots radiating from the orbit.

Young of 17 mm. show indications of adult coloration, and usually there is a dusky spot extending well onto the membranes of the anterior three dorsal spines.

Discussion. Females from north of the Gulf of Tehuantepec appear to be more strikingly marked than those from south of the Gulf of Fonseca; however, no other characters were found which would separate specimens from the two areas.

Relationship. Malacoctenus ebisui appears to be most closely related to a group in the Pacific comprised of *M. hubbsi*, *M. zacae*, *M. costaricanus*, *M. zonifer*, and *M. zonogaster*, and in the Atlantic, *M. triangulatus*. It can be distinguished from the Pacific forms by characters given in the key. It differs from *M. triangulatus* in not having the prepectoral area scaled, in its typical dorsal and anal formulae, and in coloration.

Holotype. SU 49604, an adult female, 31 mm. in standard length, from Bahia Honda, Panama. Collected by the Eastern Pacific Zaca Expedition, March 19, 1938 (original number: 28589).

Paratypes. Fifty-three specimens. Eleven parachronotopotypes: SU 49605; 15 paratopotypes: SU 49611, 49613–14; 1 from the Perlas Islands, Panama: USNM 174967; 1 from Panama: BMNH 61.8.13.32; 4 from Piedra Blanca Bay, Costa Rica: SU 49609–10; 3 from Uvita Bay, Costa Rica: SU 49612; 1 from the Gulf of Nicoya, Costa Rica: CNHM 61901; 6 from Port Parker, Costa Rica: SU 49607–08, 49699; 2 from Chamela, Jalisco, Mexico: SU 49606; 7 from Mazanillo, Colima, Mexico UMMZ 171894; 1 from Mazatlan, Sinaloa, Mexico: USNM 174964; 1 from Magdalena Island, Tres Marias: SU 49615.

Named *ebisui* for Ebisu, the patron god of the Japanese fishermen.

ZOOGEOGRAPHY

As stated in the introduction, *Labrisomus* and *Malacoctenus* are restricted to the Atlantic and eastern Pacific. Although there are no species common to both areas, the similarity of the number of species in the two areas is of interest. There are sixteen species of *Labrisomus:* eight as recognized by Hubbs (1953) in the eastern Pacific and eight as recorded in this study from the western Atlantic (one of which, *L. nuchipinnis*, is also found in the eastern Atlantic). Neither of us found subspecies indicated. I found eighteen species of *Malacoctenus:* nine in the eastern Pacific, eight in the western Atlantic, and one in the eastern Atlantic. At least eight subspecies, belonging to four

species, are indicated for the Pacific; none for the Atlantic. The zoogeographic distribution of the western Atlantic and eastern Pacific species of the genera *Labrisomus* and *Malacoctenus* are given in Figures 3 and 4 respectively. This similarity of number at the species level can be carried even further for clinid fishes. In *Paraclinus* (limited to the eastern Pacific and western Atlantic) Hubbs (1952) found six species (and six

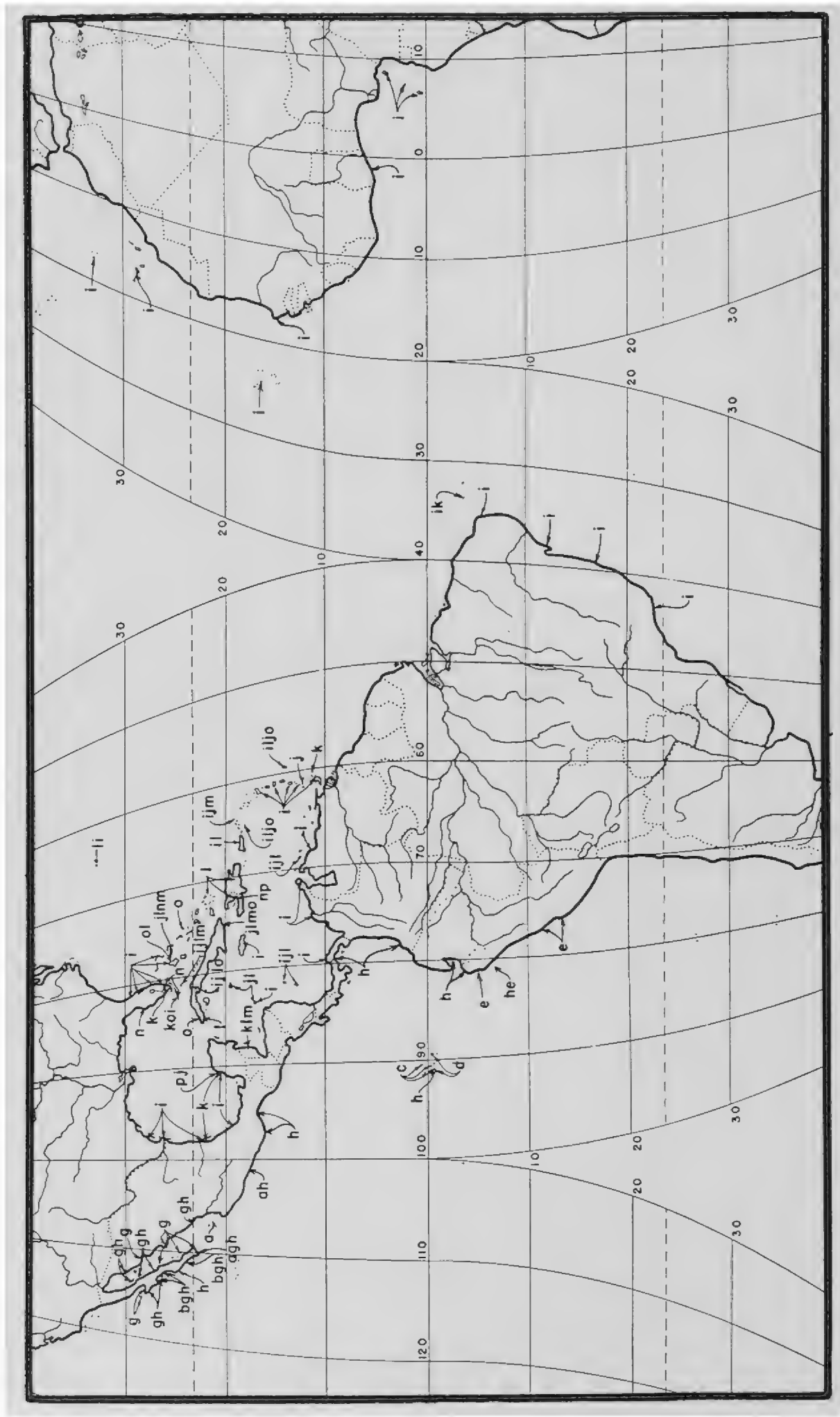


FIG. 3. Distribution of the Species of *Labrisomus* (Pacific, in part, after Hubbs, 1953).

Symbols are as follows: *L. striatus*, a; *L. wigginsi*, b; *L. dendriticus*, c; *L. jenkinsi*, d; *L. philippii*, e; *L. socorroensis*, f; *L. xanti*, g; *L. multiporosus*, h; *L. nuchipinnis*, i; *L. gobio*, m; *L. haitensis*, n; *L. nigricinctus*, o; *L. guppyi*, j; *L. kalisherae*, k; *L. bucciferus*, l; *L. albigenys*, p.

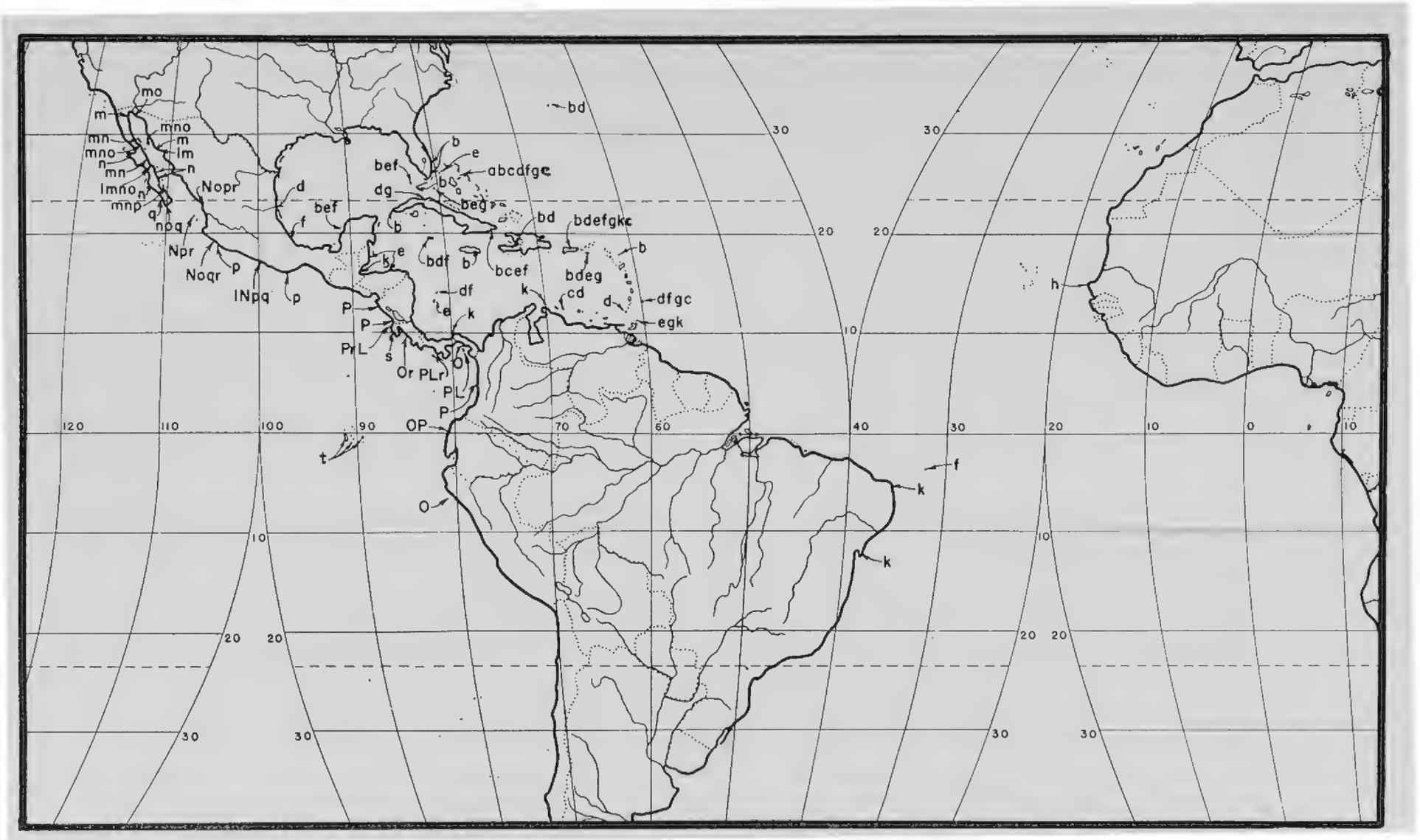


FIG. 4. Distribution of the Species and Subspecies of *Malacoctenus*.

Symbols are as follows: *M. boehlkei*, a; *M. macropus*, b; *M. erdamni*. c; *M. gilli*, d; *M. aurolineatus*, e; *M. triangulatus*, f; *M. versicolor*, g; *M. africanus*, h; *M. delalandei*, k; *M. margaritae mexicanus*, l; *M. margaritae margaritae*, L; *M. gigas*, m; *M. hubbsi hubbsi*, n; *M. hubbsi polyporosus*, N; *M. ajuerae mulaipunctatus*, o; *M. ajuerae ajuerae*. O; *M. zonifer zonifer*, p; *M. zonifer sudensis*, P; *M. zacae*, q; *M. ebisui*, r; *M. costaricanus*. s; *M. zonogaster*, t.

subspecies) in the eastern Pacific, and Springer (1955a) found six species (and no subspecies) in the western Atlantic. In *Stathmonotus* (same general geographic limits as *Paraclinus*) Böhlke (1953) listed three species (and no subspecies) in the eastern Pacific, and Springer (1955b) listed three species (and two subspecies) from the western Atlantic. The subgenera, when recognizable, serve to detract from these numerical

similarities: there are six members of the subgenus *Labrisomus* and one each of the subgenera *Brockius* and *Gobioclinus* in the Pacific, and one *Labrisomus*, two *Brockius*, and five *Gobioclinus* in the western Atlantic. Part of the importance of the above findings is that they serve as examples contradictory to the general findings of Ekman (1953) and Jordan (1905) that the tropical western Atlantic fauna is richer than the tropical eastern Pacific fauna. The clinid genera *Cryptotrema*, *Mnierpes*, *Starksia*, and *Exerpes* are found only in the tropical eastern Pacific, whereas all tropical Atlantic clinid genera are also found in the tropical eastern Pacific (pending revision of the emblemariids and chaenopsids). Meek and Hildebrand (1923) indicated the existence of a tropical eastern Pacific fish fauna considerably larger than that of the tropical western Atlantic, and Briggs (1955) found a larger number of gobiesocid species in the tropical eastern Pacific than in the tropical western Atlantic.

Pacific

Hubbs (1952), in expanding on Ekman's (1935) Panamanian faunal region, primarily used species of *Paraclinus* as indicators of tropical eastern Pacific zoogeographic provinces. He considered that area to be divided as follows: (1) a Panamanian province extending from an indefinite point in northern Peru to the vicinity of Bahia Honda, Panama, (2) a Mexican province extending from the boundary of the Panamanian province northward to a point somewhere north of Mazatlan, Sinaloa, on the mainland of Mexico, and a point near La Paz, at the southern tip of Baja California, and another point between Punta Abreojos and Port San Bartolme on the Pacific side of Baja California, and (3) a Gulf of California province with its southern limits near La Paz and somewhere north of Mazatlan.

He proposed further subdivisions of the Mexican province as follows: (1) south of Guatemala to Bahia Honda, Panama, (2) the Mexican mainland, and (3) the southern part of Baja California.

Hubbs (1953) found what he considered only partial support for his original proposals from his study of eastern Pacific *Labrisomus*. He believed the demarcations of his Mexican from his Panamanian and Gulf of California provinces to be less sharp than he had previously proposed. He also believed his knowledge of *Labrisomus* distributions in the Mexican province to be incomplete on the basis of his *Paraclinus* studies.

Briggs (1955) found what he thought were differences from the provinces as proposed by Hubbs if the boundaries were to be based solely on knowledge of gobiesocids. Briggs' data would indicate that the Mexican province should extend north of Mazatlan to Guaymas on the mainland. He interpreted Hubbs (1952) as setting a boundary "just north" of Mazatlan; whereas Hubbs' wording was "north of Mazatlan". From the data Hubbs gives on *Paraclinus*, this boundary could be interpreted as existing at Guaymas. It is unfortunate that he did not state this locality explicitly.

Information gained from the study of Pacific *Malacoctenus*, and reinterpretation of Hubbs' and Briggs' findings, results in a more uniform, although by no means completely satisfactory, concept of tropical eastern Pacific zoogeography.

In the eastern Pacific there is an area occupying approximately seven hundred miles of coastline which has its northern border roughly at Salina Cruz at the middle of the Gulf of Tehuantepec, Mexico, and its southern border approximately at the Gulf of Fonseca, Nicaragua. From available maps and literature, the coast in this area appears

to be sand, mud, mangroves, and few or no rocks. The coast extending from this area both to the north, to Mazatlan, and to the south, to perhaps Peru, is frequently interrupted by rocky areas.

A few collections (Beebe, 1938; Hildebrand, unpublished manuscript) are known to have been made from this intermediate block of coastline, and there are probably some others, but no specimens of the Clinidae, Gobiesocidae, or Tripterygiidae (Richard Rosenblatt, personal communication) have ever been reported from there.

This Central American gap separates the subspecies of several sedentary forms: *Malacoctenus a. afuerae* from south of the gap and *M. a. multipunctatus* from the north; *M. z. sudensis* from south of the gap and *M. z. zonifer* from the north; *M. m. margaritae* from south of the gap and *M. m. mexicanus* from the north. Hubbs (1953) reported distinctions between populations of *Labrisomus multiporosus* from either side of the gap (*L. multiporosus*, which occupies the most northern locality of those species of *Labrisomus* found south of the gap, reaches north, in that area, only to middle Panama). *Malacoctenus hubbsi*, *M. zacae*, and *Labrisomus striatus* are not found further south than the northern border of the gap, and *M. costaricanus* is not known to reach north to its southern boundary. Al-Uthman (1955) found that an undescribed species of the clinid genus *Brannerella* was separated into two morphological types which had their limits north and south of the gap respectively (a third morphological type was described from the Galapagos). Richard Rosenblatt informs me that there are several closely related tripterygiids which occur only on one side of the gap or the other. Ginsburg (1947) described *Bathygobius r. curticeps* from north of the gap and *B. r. ramosus* from south of it; he did, however, group a small sample of specimens from Ecuador and Peru with the northern form. Ginsburg (1953) also describes *Dormitator l. mexicanus* from north of the gap and *D. l. latifrons* from south of it. Only two gobiesocids (*Tomicodon petersi* and *Gobiesox adustus*) are considered by Briggs (1955) to be undifferentiated on either side of the gap. Of nine other species inhabiting the mainland coast of the tropical eastern Pacific, eight are restricted to areas either to the north or to the south of the gap, and one (*G. papillifer*) is separated into different subspecies on either side of the gap.

There is also evidence from the invertebrate fauna which suggests that the gap is real. Bayer (1953) found no species of the coelenterate family Gorgoniidae from the area of the gap. The relationships between the species from the two areas on either side were not mentioned. Ekman (1953) gives similar distributions for the crab genus *Mithrax* (after Rathbun, 1925). A perusal of Rathbun's paper indicates that many of the species are the same from either side of the gap; however, it must be pointed out that the systematics of infraspecific categories in marine invertebrates has received little attention.

In light of the above evidence a southern boundary for the Mexican Province would be placed in the region of Tangola-Tangola Bay, as suggested by Briggs (1955). The northern limit of the Panamanian Province would be shifted to the Gulf of Fonseca. The area between these two points should perhaps be defined separately, for which I propose the name "Pacific Central American Faunal Gap."

There are two clinids which are apparently undifferentiated on either side of the Gap: *Malacoctenus ebisui* and *Paraclinus mexicanus*, although there appear to be subtle differences in color between specimens from the two localities in the first of these. Nonsedentary forms do not appear to be affected by the gap.

If the "vacuum" of the gap as defined above is an artificial one, it can at least be surmised that there is a quick change from the Panamanian to the Mexican provinces in that area.

There is some paleogeological information which may have bearing upon the problem. Schuchert (1955), in his paleogeological map of the Miocene, indicates an area between what are now the limits of the Gulf of Tehuantepec, through which the Atlantic and Pacific were joined (Not all geologists agree that a Tehuantepec oceanic bridge existed. See Durham, Arellano, and Peck, 1952). A second oceanic connection is shown occupying an area roughly between the Gulf of Fonseca, Nicaragua, and the Gulf of Chiriqui, Panama. The first channel was supposedly present during upper Miocene and lower Pliocene, and the second during lower and middle Miocene (Schuchert, 1935), although the possibility of the two having been for a short period contemporaneous is not negated. An area of coastline is situated between these two channels which is almost identical with that of the faunal gap proposed here. This mass of land was most probably continuous with Jamaica in the Atlantic (Schuchert, 1955). What the marine faunal distributions were during Miocene times cannot be told from present knowledge, but it is commonly believed that specific differences between the tropical Atlantic and Pacific fauna in this hemisphere did not occur until after the oceanic bridges had ceased to exist in either upper Miocene or lower Pliocene. Infraspecific differences (or in some cases specific differences) on either side of the Gap would have occurred after the oceanic connections had been closed for some time. This explanation still leaves unanswered the problem of how the species were able to maintain their integrity in earlier times in the areas on either side of the Gap, unless no barrier to gene dispersal was present. There is no reason, on the basis of known geology, to suspect that the coast was ecologically different in Miocene-Pliocene time than at the present. Mountain building had already established a rocky coast north and south of the Gap by the Miocene. The mountains of the inland area comprising the Gap are of recent development and do not extend onto the coast as do the older northern and southern ranges.

As stated above, Mazatlan is the approximate northern end of the rocky coast on the Mexican mainland south of the Gulf of California. From Mazatlan to Guaymas, on the mainland, the coast consists primarily of mangroves and river deltas. From Guaymas, which is rocky, north to Punta Peñasco the coast is sandy in nature with isolated rocky points, the most northern of which is Punta Peñasco. The extreme northern end of the Gulf is occupied by the delta of the Colorado River. The entire Gulf coast of Baja California can be considered essentially rocky, as are the numerous islands of the Gulf. This is also true for much of the Pacific coast of the peninsula. For the purposes of this study the Pacific coast is important only as far north as Bahia Sebastian Vizcaino, where considerable cold-water upwelling occurs. This upwelling acts as a demarcation line between the tropical and temperate eastern Pacific faunas of the northern hemisphere. I am informed (Dr. B. W. Walker), however, that most of the tropical forms drop out at a point further south, Bahia Magdalena.

My findings agree with those of both Hubbs (Mazatlan) and Briggs (Guaymas) for the northern boundaries of the Mexican province.

Mazatlan is the northern limit for *M. z. zonifer*, *M. hubbsi polyporosus*, *M. zacae*, *M. ebisui*, and probably *Labrisomus striatus* on the Mexican mainland. Guaymas is the northern limit of *M. margaritae mexicanus* and the southern limit for *M. gigas* and *M. h. hubbsi* on the mainland. The area between Mazatlan and Guaymas is devoid of clinids

(and gobiesocids), except for a single specimen of *L. xanti* known from Topolobampo Bay. The area between Mazatlan and Guaymas has probably acted as the isolating barrier separating *M. hubbsi* into two subspecies.

Workers at the University of California at Los Angeles, inform me that there are many species of different ecological requirements which are separated by the Mazatlan-Guaymas faunal gap.

Malacoctenus afuerae multipunctatus and *Labrisomus multiporosus* exceed both of the boundary lines for the northern limits of the Mexican province.

On the Gulf coast of Baja California, *M. z. zonifer* reaches Espiritu Santo Island, but *M. zacae* and *L. striatus* scarcely reach the mouth of the Gulf.

The northern limit of the Mexican province on the Pacific coast, Bahia Sebastian Vizcaino, is reached by *L. xanti, L. multiporosus,* and *M. h. hubbsi.*

The Gulf of California province is represented in this study by only one endemic *Malacoctenus, M. gigas;* as are the Galapagos Islands with only one species of *Malacoctenus:* the endemic *M. zonogaster.*

Atlantic

Results of the present study agree with Ekman (1953) in indicating that the tropical western Atlantic is essentially a single zoogeographic unit without notable subdivisions. The coasts of Central and South America, the Gulf of Mexico, and Bermudas have a paucity of species as compared to the coasts of southern Florida, the Bahamas, and the Antillean chain, and no species are present in the former areas which are not found in the latter. Only one labrisominid occurring in this region, *M. delalandei* is not known from above 20° N. latitude. Of the sixteen species of labrisominids in the western Atlantic, the largest number, thirteen, are known from the northern Bahamas, and one, *M. boehlkei,* is known only from that area. This concentration of species compared to the number known from the eastern Antillean chain may be an artifact of collecting, although Erdman (1957) notes a general decrease in the number of fish species from the West Indies as one proceeds from west to east. Because of the extreme distance separating the Bermudas from other tropical coastlines, a paucity of tropical fish species in those islands is not to be unexpected.

There are three areas which are not known to have clinid faunas. These are the coastlines of the northern Gulf of Mexico, northern South America between eastern Venezuela and Natal, Brazil, and between eastern Honduras and middle Panama. All of these are characterized by the presence of any or all of the following: large river deltas, mud, sandy beaches, and mangroves. These areas do not appear to have an isolating effect on the populations on either side of them as the currents of the region wash all shores from south to north and are able to distribute the planktonic larvae of some of the species throughout the region. An example of this is well demonstrated by the sandy coasts of northern Mexico and Texas which are not proper habitats for labrisominids. About seventy years ago rocky jetties were built at Brownsville, Port Aransas, and Galveston, Texas, providing a suitable habitat in these areas for the first time. The jetties at the first two localities are now inhabited by *Labrisomus nuchipinnis;* those at Galveston do not support any clinids, possibly because of the low salinities of this locality.

The most interesting element of the Atlantic labrisominid fauna is *L. nuchipinnis.* This species has the widest distribution of any known clinid and exceeds the ranges of any of the other clinids in the area it occupies. It is interesting to note that *L. multi-*

porosus, the nearest relative of *L. nuchipinnis*, has the widest distribution of any Pacific *Labrisomus* species.

Within the tropical western Atlantic, variation does occur in several of the labrisominid species. Such variation is most notable in *L. nuchipinnis*, *L. haitiensis*, *M. macropus*, *M. erdmani*, and *M. gilli*, but there is no discernible geographic pattern to this variation which would afford an explanation for it.

Only two clinids are found in the tropical eastern Atlantic, *L. nuchipinnis* and the endemic *M. africanus*. The range of the former shows only slight agreement with the limits of the tropical eastern Atlantic as given by Ekman (1953, after W. Michaelson; reference not given): Cape Verde Islands to Mossamedes, Angola. *Labrisomus nuchipinnis* is known from as far north as the Madeira Islands and only as far south as Annobon Island. This latter limit is of interest as it lies in the area where the warm Guinea Current from the north meets the cold Benguela Current from the south and together leave the coast as the South Equatorial Current.

The problem arises as to the locality or origin of *Labrisomus* and *Malacoctenus*. The absence of living species or fossils from the Indo-Pacific probably indicates their absence from that region at any time. The presence of a Miocene fossil, *Labrisomus pronuchipinnis* Arambourg (1921, 1927), from the Mediterranean coast would tend to support Steinitz (1950) conclusion that *Labrisomus* on the African coast is a Tethys relic. Further support for this argument would be the endemic *Malacoctenus africanus*, known only from Dakar. The former existence of a uniform Tethys fauna would still not explain how species crossed the Atlantic. The predominent east-to-west flow of the oceans would favor an African origin, but the significantly larger American fauna would indicate a center of origin in this hemisphere. Hubbs (1953) believes that *Labrisomus*, with a long pelagic larval stage, crossed from Brazil to Africa via an equatorial counter-current. If this is true, we are still in need of an explanation for the distribution of *Malacoctenus* which apparently does not have planktonic larvae (specimens of 10 or 12 mm. are collected with adults). It is interesting that Cadenat (1950) reports numerous predominantly western Atlantic fishes from the west African Coast, and Burkenroad (1939) reports that the western Atlantic shrimp, *Penaeus duorarum* is also found on the west African coast. Because of the presence of a Miocene fossil *Labrisomus*, crossings would have to have occurred prior to, or during, the Miocene. The presence or absence of a counter equatorial current at that time is not known, neither is the mechanism allowing *L. nuchipinnis* to remain undifferentiated on either side of the Atlantic. Further speculation on these matters is considered useless until more historical and oceanographic evidence is available.

Summary

The subtribe Labrisomini is comprised of the genera *Labrisomus* and *Malacoctenus*. These fishes are sedentary and predominantly restricted to the rocky coasts and coral reefs of the tropical marine waters of the western hemisphere. A systematic revision of these genera reveals the existence of sixteen species, and no subspecies, of *Labrisomus*, and eighteen species, and eight subspecies, of *Malacoctenus*.

The following taxa are described as new: *Malacoctenus boehlkei* and *Malacoctenus triangulatus* from the western Atlantic; *Malacoctenus hubbsi hubbsi*, *Malacoctenus hubbsi polyporosus*, *Malacoctenus margaritae mexicanus*, *Malacoctenus gigas*, *Mala-*

coctenus afuerae multipunctatus, Malacoctenus zonifer sudensis, Malacoctenus zacae, Malacoctenus costaricanus, and *Malacoctenus ebisui* from the eastern Pacific.

No species of either *Malacoctenus* or *Labrisomus* are common to both the Atlantic and Pacific.

The present study indicates five expanses of coastline in this hemisphere which are devoid of clinid fishes, as well as other groups of sedentary fishes and invertebrates: 1) between Guaymas, Sonora, Mexico, and Mazatlan, Sinaloa, Mexico, 2) between the middle of the Gulf of Tehuantepec, Oaxaca, Mexico, and the Gulf of Fonseca, Nicaragua, 3) the northern coast of the Gulf of Mexico, 4) the Atlantic coast between eastern Honduras and central Panama and 5) the coast between eastern Venezuela and Natal, Brazil. All of these sections of coastline are characterized by the presence of river deltas, sand, mud, or mangroves; conditions unsuitable as clinid habitats. The first two areas listed act as barriers to gene dispersal since several species are represented on either side of their boundaries by subspecies; other species do not exceed either one or the other of their boundaries.

On the basis of the present study the northern limit of the Panamanian marine faunal province is located at the Gulf of Fonseca, Nicaragua, and the southern limit of the Mexican marine faunal province is placed at about the middle of the coast of the Gulf of Tehuantepec, Mexico. For the area between these two localities is proposed the name "Pacific Central American Faunal Gap." The present study indicates that the northern boundary of the Mexican marine faunal province on the Mexican mainland can be placed at either Mazatlan, Sinaloa, or Guaymas, Sonora, depending upon the species used as indicators.

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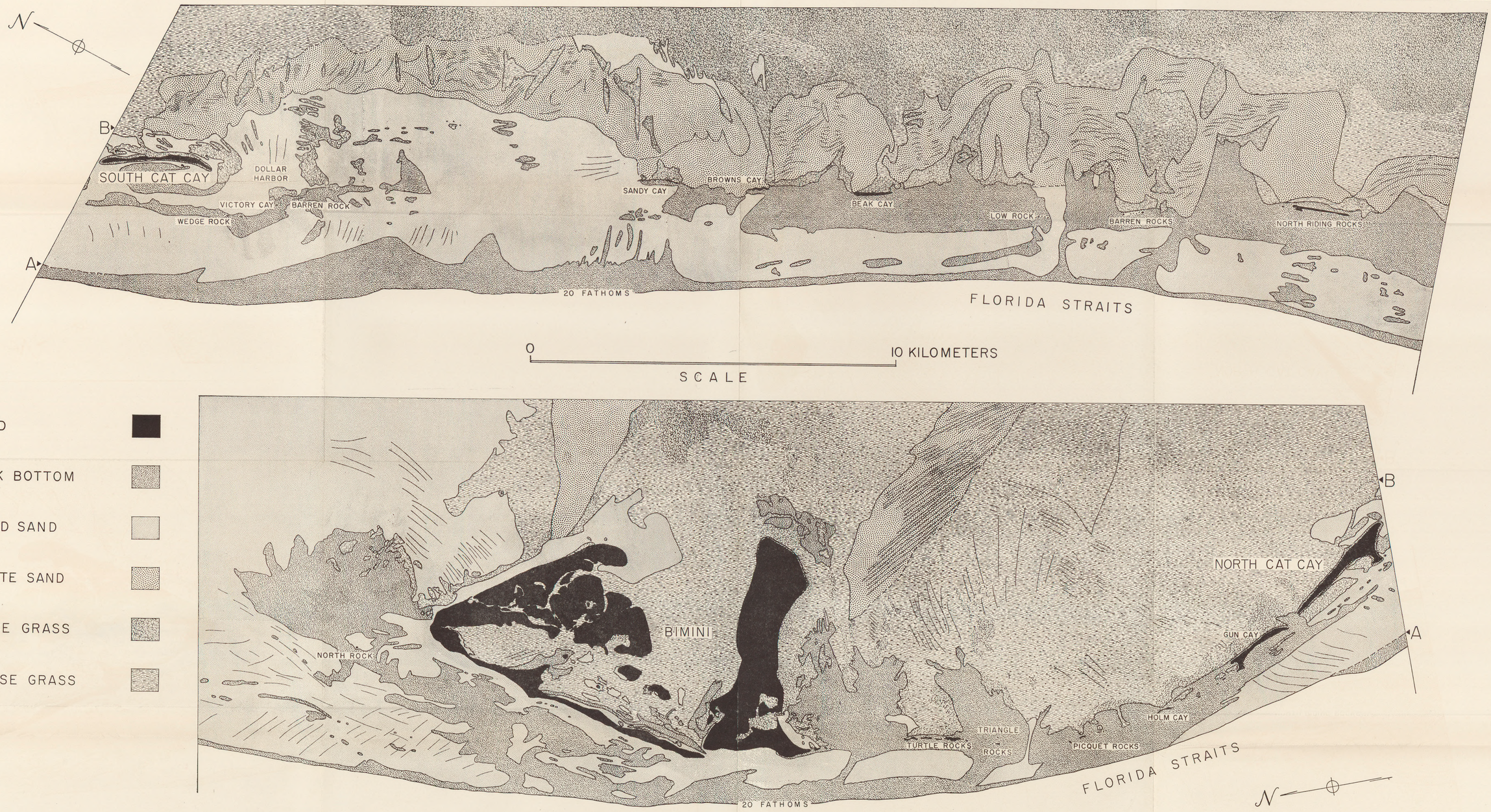

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